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DO I NEED A BODY TO KNOW WHO I AM? NEURAL MECHANISMS OF BODY OWNERSHIP

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To the two most inspiring women in my life:
my mother Maria and Ibu Luh Sugati

ABSTRACT

The feeling that our body belongs to us, and that it is an essential part of ourselves, is a fundamental aspect of human self-awareness and individual psychological identity. The intimate relation between the sense of body ownership and the sense of self emphasizes the importance of understanding the former in order to access and comprehend the latter. However, it also outlines the challenge of objectifying the body by turning it into a subject of controlled experimental research.

The aim of this thesis was to create an experimental tool with which to overcome this immanent hindrance and study for the first time the mechanisms underlying the feeling of an entire body as belonging to oneself. Three studies, designed to address the perceptual and neural underpinnings of full-body ownership, are presented.

In **Study I** we created a perceptual illusion in which healthy participants experience a whole artificial or real body as their own. This illusory sensation is elicited when participants perceive convergent multisensory input from their own body (which is out of view) and the new body (which they view from a first person perspective). Importantly, the feeling of ownership was not confined to the specific location of sensory stimulation, but instead encompassed the entire body. The illusory perception was abolished or significantly diminished when the input from the different sensory modalities was temporally desynchronized, or when the new body was replaced by a non-corporeal object of similar size. In sum, this first study showcases a novel experimental set-up that enables the scientific study of the perceptual mechanisms underlying full-body ownership, and provided evidence that in the core of this perceptual phenomenon lies the integration of convergent multisensory input from the body.

In **Study II** we specifically investigated the role played by the visual perspective in the generation of a full-body ownership illusion. To that end, we compared the strength of the illusion when the new body was perceived either from a first person or from a third person perspective. The results indicated that attributing a new body to oneself is possible only when one perceives this body, and the multisensory signals deriving from it, from an egocentric (i.e. first person) perspective.

In **Study III** we created an experimental set-up to induce the full-body illusion in a functional magnetic resonance imaging (fMRI) setting, which enabled us to shed light on the neural mechanisms underlying full-body ownership. In three independent fMRI experiments we specifically investigated (i) which neural activation is associated with the experience of full-body ownership, (ii) whether the multisensory processes giving rise to the full-body illusion operate in body-centered reference frames, and (iii) how ownership of individual body parts translates into the unitary experience of owning a whole body? We found that perceiving a body as one's own is associated with increased activity in the ventral portion of the bilateral premotor areas, the anterior part of the left intraparietal sulcus and the left putamen. In addition, the activation in the ventral premotor cortex was found to reflect the construction of ownership of a whole body from its parts. In fact, it was stronger when the stimulated body part was attached to the body, present irrespective of the location of the stimulation evoking the illusion, and moreover displayed multivoxel patterns carrying information about full-body ownership. All together these findings suggest that the unitary experience of owning an entire body is produced by neuronal populations that integrate multisensory information across body segments in body-centered reference frames.

LIST OF PUBLICATIONS

I. **Petkova VI** and Ehrsson HH. If I were you: perceptual illusion of body swapping. *PLoS One* (2008), 3(12):e3832

II. **Petkova VI** & Khoshnevis M, and Ehrsson HH. The perspective matters! Multisensory integration in ego-centric reference frames determines full body ownership (2011) *Front. Psychology* 2:35.

III. **Petkova VI**, Björnsdotter M, Gentile G, Jonsson T, Li TQ, Ehrsson HH. From part to whole-body ownership in the multisensory brain. *Current Biology* (2011) 21 1-5.

LIST OF ADDITIONAL PUBLICATIONS

I. **Petkova VI** and Ehrsson HH. When right feels left: referral of touch and ownership between the hands. *PLoS One* (2009), 4(9): e6933

II. **Petkova VI** and Ehrsson HH. Body self-perception. McGraw-Hill 2010 Yearbook of Science & Technology, McGraw-Hill Professional, New York (2010), 50-53

III. Gentile G, **Petkova VI**, Ehrsson HH. Integration of visual and tactile signals from the hand in the human brain: An fMRI study. *J Neurophysiology* (2011) 105(2):910-22.

IV. Guterstam A & **Petkova VI**, and Ehrsson HH. The illusion of owning a third arm. *PLoS One* (2011) Feb 23; 6(2): e1720

V. Brozzoli C & Gentile G, **Petkova VI**, Ehrsson HH. fMRI-adaptation reveals a cortical mechanism for the coding of space near the hand. *J. Neurosci.* (2011) 31(24) 9023-9031.

VI. **Petkova VI** & Zetterberg H, and Ehrsson HH. Rubber hands feel touch but not in blind individuals. *PLoS One* (under review)

CONTENTS

LIST OF ABBREVIATIONS

ANOVA	Analysis of variance
BOLD	Blood-oxygen-level-dependent
EBA	Extrastriate body area
fMRI	Functional magnetic resonance imaging
HMD	Head mounted displays
IPS	Intraparietal sulcus
LOC	Lateral occipital cortex
PMd	Dorsal premotor cortex
PMv	Ventral premotor cortex
RF	Receptive field
RHI	Rubber hand illusion
SCR	Skin conductance response
STS	Superior temporal sulcus
TPJ	Temporo-parietal junction

1 INTRODUCTION

> *"The aspects of things that are most important for us are hidden because of their simplicity and familiarity. (One is unable to notice something because it is always before one's eyes.)The real foundations of this enquiry do not strike a man at all."*
>
> *Ludwig Wittgenstein, Philosophical Investigations*

Since ancient times, philosophers have cogitated about the very essence of our being, with the aim to unravel the complex relationship between the mind and the body. Ever since then, through continuous development of philosophical theories as well as perpetual progress in medicine and science, the concept and nature of our bodily existence has been repeatedly redefined and reconceived. Historically, the body has mostly been conceptualized and analyzed with respect to the mind, and conceived in numerous differential ways such as: A substance from which the mind is derived (Aristotle, Hobbs, Hegel) or which is derived from the mind (Berkeley, Leibniz, Schopenhauer); An "extended" substance which together with the mind represents God (Spinoza) or which interacts with the mind in the pineal gland (Descartes); A non-conceptual form of knowledge (Kant), different from any other type of knowledge, but a necessary prerequisite for other types of knowledge (Merleau-Ponty 2005); The "storm-center" of experience (James 1890); and The point of origin of psychological identity (Cassam 1997; Edelman 2004). Only more recently, the focus of philosophical and scientific interest shifted from the mind-body interplay and the body's constituents, to the actual mechanism underlying the intimate experience of our corporeal self (Bermudez et al 1998; Gallagher 2005).

This thesis is a modest attempt to contribute to our current understanding of the processes that lead to the experience of perceiving a body as belonging to oneself. It is a quest for answers to some apparently simple, yet unresolved questions such as: What are the perceptual and neural mechanisms that allow us to experience our bodies as part of ourselves? How come we experience the body as a unified whole rather than a set of fragmented parts? Does the mind have the capacity to attribute an entire new body to the self?

Before we tackle these problems however, we need to address the following three fundamental questions, which will set the scene for the studies outlined in this thesis and the hypotheses behind them: What is body ownership? Why study body ownership? How can body ownership be studied?

1.1 WHAT IS BODY OWNERSHIP AND WHY STUDY IT?

In science, especially within the cognitive domain, it is imperative to precisely define the concepts under investigation, in order to avoid any erroneous interpretations or misleading conclusions. The concept of body ownership is very complex by nature, and its definition depends on the scientific or philosophical angle of observation and approach. For example, in philosophy the term body ownership is most often primarily related to the intimate nature of bodily sensations (i.e. pain, touch), and their relation to human consciousness (i.e. the concept of qualia). In clinical psychology and psychiatry, the focus is frequently on personality and pathological disturbances thereof, which can result in dysfunctional perception of the own body (e.g. body integrity identity disorder, body dysmorphic disorder, eating disorders, depersonalization disorder, schizophrenia, out-of body experiences etc.). In the medical sciences, the term body ownership is often referred to in relation to ethical aspects of organ donation, whereas in experimental psychology, this concept has been addressed in the context of experimental investigations of visual self recognition, proprioception, and recently, in the context of multisensory body representation (see below).

In the current thesis, the term body ownership is used to describe the sensation of experiencing a body as belonging to oneself. In fact, the studies presented below were specifically designed to address the perceptual and neural mechanisms underlying this fundamental process of attributing a body to the self.

Shedding light on the mechanisms that drive our experience of a corporeal self represents a crucial step towards a deeper understanding of our intimate experience of a self in more general terms. That is, understanding the perceptual and neural mechanisms that enable us to attribute our body to our self could help us reveal the mechanisms that give rise to the qualia of the embodied self. In addition, apart from being a way to scientifically address a long standing philosophical question, the understanding of the neural underpinnings of body ownership is also highly relevant for extending our knowledge of the fundamental working mechanisms of the human brain.

Moreover, as will be described in much detail in this thesis, in the course of addressing these questions we developed a novel experimental setup that allows one to induce people to perceive a whole new body as their own. This experimental setup lends itself for a wealth of future potential applications in scientific, clinical as well as industrial settings.

1.2 HOW CAN BODY OWNERSHIP BE STUDIED?

A utopian experiment aimed at investigating the principles of body ownership, would be designed in a way that allows the comparison between the experience of owning a body to the experience of not owning one. However, the concept of a brain in a “life-support vat” is only possible in the realm of science fiction or philosophy (Dennett 1978).

“That same old body always there”, as famously stated by William James in his Principles of Psychology (1890), pinpoints the difficulty in objectively studying the mechanisms that allow us to experience a body as our own. The body is always there, as is the intimate sensation of belonging to it, and this poses fundamental challenges to any attempt of its scientific investigation.

Faced with these inherent difficulties, most of the early research efforts focused on delineating some of the more tangible aspects of the body that could be systematically studied. Within this context, one aspect that emerged was a subdivision of different aspects of body representation, which is still applied today. Two of these aspects are the body image and the body schema (Gallagher 1986). The body image refers to the perceptual experience of the body, the general conceptual understanding of it, and the emotional attitudes one has towards it. In contrast, the body schema refers to a non-conscious collection of processes that registers the body’s spatial and motor properties

(Gallagher 2005; Gallagher and Cole 1995; Graziano and Botvinick 2002; Haggard and Wolpert 2005; Head and Holmes 1911). However, this line of research did not pertain to the specific problem of body ownership.

Neurology

The first more direct evidence for the neural underpinnings of the corporeal self came from neurological studies of patients with somatoparaphrenia. This condition usually manifests in patients with distributed cortical and subcortical lesions, and is characterized by delusions concerning the contralesional paralyzed body parts. Such delusions typically include feelings of "non-belonging" towards certain body parts, as well as the tendency to attribute parts of the own body to someone else (Baier and Karnath 2008; Feinberg et al 2010; Gandola et al 2011; Karnath et al 2005). Most data on this peculiar body disownership condition has been derived from single case reports, which have attributed the symptoms to extended right fronto-temporo-parietal lesions (Vallar and Ronchi 2009). However, some single case studies have also reported more focal cortical or subcortical lesion locations (e.g., right basal ganglia, thalamus and subcortical white matter; (Bisiach et al 1991; Halligan et al 1995; Healton et al 1982).

Neuroimaging studies on somatoparaphrenia have reported inconsistent findings. For example, Feinberg et al (1990) attributed this condition to lesions in the supramarginal gyrus (Feinberg et al 1990), the posterior corona radiate (Feinberg et al 1990) and in a more recent study also right medial and orbito-frontal areas (Feinberg et al 2010). In contrast, (Baier and Karnath 2008) associated it with a lesion in the right posterior insula. In both studies however, there was lack of control for anosognosia for hemiplegia (a condition in which a person who suffers paralysis after a brain stroke seems unaware of the existence of his or her disability). In a recent study, (Gandola et al 2011) addressed this issue and found that spatial neglect and anosognosia for hemiplegia were associated with wide spread lesions in the fronto-temporo-parietal network. In contrast, patients with somatoparaphrenia showed an additional extensive lesion in white matter and subcortical structures, i.e. the thalamus, basal ganglia and amygdala. According to the authors' hypothesis, lesions to these latter structures might prevent most sensory input from being processed in neocortical structures, and in turn lead to the reduced sense of familiarity experienced by somatoparaphrenic patients for their paralyzed limbs.

Taken together, these contrasting findings of case studies of somatoparaphrenia make it difficult to draw any definite conclusions about the neural basis of body ownership. Nevertheless, these studies were the first to suggest a link between different brain structures and the feeling of body ownership.

Experimental psychology

A real breakthrough in the experimental investigation of body ownership came with the discovery of the rubber hand illusion (RHI) (Botvinick and Cohen 1998), in which healthy participants are induced to perceive an artificial hand as belonging to themselves.

The use of illusions to study the processes underlying normal perception is not a novel concept in the context of psychology research. In fact, some important insights into the basic mechanisms underlying various aspects of physiology, visual perception and cognition, have been gained through illusions such as the Hermann grid illusion, the Necker cube, the Rubin vase, Muller-Lyer illusion, the Ponzo illusion, Kanizsa triangle, the Esher's paradox illusions, the Cutaneous rabbit illusion, and the Pinocchio illusion, to name only a few.

The RHI pioneered the systematic investigation of the principles behind the attribution of a limb to the self, as it was the first experimental tool to enable the systematic manipulation of the experience of limb ownership. That is, while still not fulfilling the conditions of the utopian body ownership experiment mentioned previously, the RHI enables at least a single artificial limb to be perceived as either belonging to oneself or not. For the induction of the illusion, synchronous touches are applied to the participants' real hand which is out of view, and a rubber hand which is in full view (Figure 1). If the visuo-tactile stimulation occurs in temporal and spatial synchrony, the illusion typically starts within ten to fifteen seconds. Conversely, if the rubber hand is rotated with respect to the real hand, replaced by a non-corporeal object, or touched out of synchrony with the real hand, the illusion breaks down (Armel and Ramachandran 2003; Botvinick and Cohen 1998; Costantini and Haggard 2007; Durgin et al 2007; Ehrsson et al 2005; Ehrsson et al 2004; Ehrsson et al 2007; Holmes et al 2006; Kanayama et al 2007; Lopez et al 2008; Makin et al 2008; Pavani et al 2000; Rorden et al 1999; Tsakiris and Haggard 2005; Tsakiris et al 2007a).

In sum, in behavioral terms, studies on the RHI have demonstrated how temporal and spatial patterns of congruent visual and somatosensory signals in hand-centered reference frames, play an important role in how we come to experience that a limb is part of our own body.

Figure 1. Experimental set-up used to induce the rubber hand illusion. The participant's right hand is placed behind a precluding wall. A life size cosmetic upper limb prosthesis is placed in front of the participant in alignment with the participant's hidden right hand. Two identical brushes are used to apply either synchronous (experimental condition) or asynchronous (control condition) strokes on identical locations of the two hands. The participant is asked to fixate the brush strokes on the rubber hand.

Neuroscience

Neuroimaging studies implementing the RHI, have demonstrated that the embodiment of the rubber hand is associated with increased activity in the ventral portion of the bilateral premotor cortices, the anterior section of the left intraparietal sulcus (Ehrsson et al 2005; Ehrsson et al 2004) (Figure 2) and the right posterior insula (Tsakiris et al 2007a). An important study has shown that the rubber hand is indeed fully incorporated in the body as threats towards the rubber hand as well as threats to the participant's own hand lead to similar increase in responses in the insula and the anterior cingulate cortex (Ehrsson et al 2007), i.e. brain regions associated with anxiety and interoceptive awareness (Critchley et al 2003; Ploghaus et al 1999; Wager et al 2004).

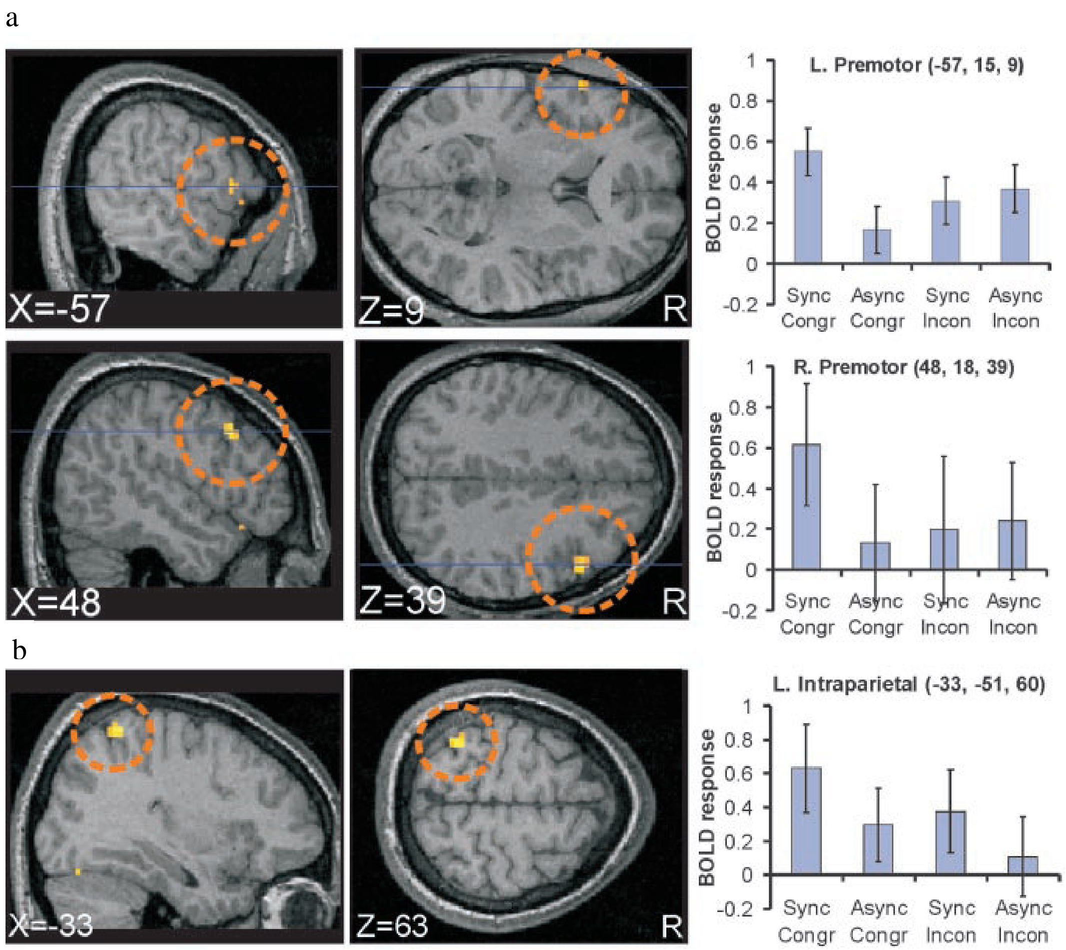

Figure 2. **(a)** Bilateral premotor activity that reflects the rubber hand illusion (interaction effect, *P* <0.005 for display purposes). The activation peaks are located in the inferior part of the precentral sulcus. R denotes right; coordinates in standard space are indicated at lower left. The plot shows the contrast estimates; error bars denote SEs. **(b)** Intraparietal activity that reflects the effects of both seeing the arm in a congruent position and perceiving synchronous brushstrokes (conjunction of the main effects, *P* < 0.001 in each contrast).
(Reprinted with permission by the authors).

Insights from electrophysiological studies in non-human primates

The body is a multisensory construct, as is the vast majority of things we perceive or act upon in our life. Hence, in order to interact with the environment our nervous system needs to be able to integrate the different sensory inputs originating from various objects into meaningful percepts. A seminal study conducted on monkeys, characterized the properties of a type of neurons located in the ventral premotor cortex that responded to visual stimuli near the body, (i.e. that are within reach), and whose visual receptive fields (RFs) and tactile RFs were spatially aligned (Rizzolatti et al 1981) [see also (Sakata et al 1973)]. Subsequent studies have then revealed the existence of an entire network of brain areas with similar multisensory neurons that respond to visual, tactile and proprioceptive stimulation. This network includes the ventral premotor cortex (Cooke and Graziano 2004; Fogassi et al 1996; Graziano 1999; Graziano et al 1997), the ventral intraparietal area (Avillac et al 2007; Avillac et al 2005; Bremmer et al 2001; Colby et al 1993; Duhamel et al 1997; Duhamel et al 1998; Graziano et al 2000; Iriki et al 1996; Schlack et al 2005), and the putamen (Graziano and Gross 1993). Crucially, the multisensory neurons in these areas have also been found to have visual RFs centered on the monkeys' head, face, neck, torso, shoulders, arms or hands that overlap considerably with their tactile RFs (Avillac et al 2005; Fogassi et al 1996; Gentilucci et al 1983; Graziano et al 1997; Ishida et al 2010). Furthermore, their visuo-tactile RFs are anchored to a specific limb or body part, so that when the limb or body part moves, the visual RFs of the bisensory neurons move along with it (Fogassi et al 1996; Graziano 1999; Graziano et al 2000; Graziano and Gross 1993; Graziano et al 1997). Importantly, the alignment of the visual and tactile RFs occurs regardless of the position of the eyes of the monkey (Graziano 1999). In other words, these neuronal populations are likely to represent a key factor for coding visual information in near personal space within body-part-centered coordinate systems. Of particular interest are recent neuroimaging studies in humans that have documented the existence of similar multisensory integration occuring in near personal space, and found it to be associated with activity in the premotor cortex, the anterior portion of the intraparietal sulcus and the putamen (Brozzoli et al 2011; Gentile et al 2011; Makin et al 2007).

Beyond mere limb ownership

The RHI has been a highly influential scientific model, both because it initiated an avalanche of experimental research aimed at unveiling the perceptual, cognitive and neural underpinnings of the attribution of a limb to oneself, and because it gave researchers the means to address other fundamental questions that had previously been beyond access.

Some of these questions relate to the perceptual constraints of the overall bodily morphology. For example, it has been shown that humans do not have the capacity to embody a non-corporeal object that does not sufficiently resemble the general shape of a human hand (Tsakiris et al 2010a) (but see (Armel and Ramachandran 2003) for contradictory results). However, more recent studies have challenged the idea of a rigid body morphology, by demonstrating that healthy individuals can be induced to experience simultaneous ownership over three arms (Ehrsson 2009; Guterstam et al 2011). Further research would be needed to unravel the exact limits of the plasticity of the body representation.

Other questions have bearings on important clinical and industrial applications. For example, Ehrsson et al (2008) showed that amputees can also be induced to experience the rubber hand illusion, with the artificial hand "replacing" their phantom hand (Ehrsson et al 2008). Subsequent lines of research focused on the development of robotic hand prosthesis with tactile feedback, which provide amputees with actual sensory feedback from the artificial hand (Antfolk et al 2010; Rosén et al 2009). In parallel lines of research, studies with healthy individuals have shown that participants can perceive ownership of computer-animated hands (Perez-Marcos et al 2009; Sanchez-Vives et al ; Slater et al 2008), setting the scene for further development of brain-computer interface, tele-presence and tele-robotics.

A further category of questions pertain to basic physiological principles of human higher order perception. For example, systematic manipulation of the extent of temporal discrepancies between the visual and tactile input driving the RHI, has demonstrated that a time window of less than 300 ms is critical for multisensory integration to occur (Shimada et al 2009). In a similar line of research, scientists have used the RHI to investigate the weighting of the sensory signals when multisensory input is integrated into a unique percept. Another study used a cross modal effect of visual distracters on tactile judgments (Spence et al 2000) showing that the visual input during the RHI dominates over proprioception and kinesthesia and leads to mislocalization of touch (Pavani et al 2000). The dominance of vision over touch has been further demonstrated in experiments employing the RHI which showed that the experience of the illusion is possible even when the visual input contradicted the tactile input properties (i.e. smoothness) (Schutz-Bosbach et al 2009).

Of utmost scientific importance is the fact that in more recent studies the principles of the RHI were extended beyond the realm of hand ownership as such, and used to address more general questions that have bearings on personal identity and the relation between the self and the body. For instance, by applying the same type of synchronized visuo-tactile stimulation, recent studies have demonstrated that healthy participants can be induced to attribute even the face of another individual to themselves (Sforza et al 2010; Tsakiris 2008). In these experiments, participants observed a photograph of a face on a computer screen. Crucially, the photograph could either depicted their own face, someone else's face, or a morphed face in which the degree of 'self' and 'other' was systematically and gradually manipulated from 100% self to 100% other. In the experimental condition, in which the participants' face was touched in synchrony with the face they were observing on the computer screen, participants attributed the seen face to themselves even in the conditions in which the morphed face was less than 50% self.

Similarly, other researchers have been able to use the basic principle of the RHI to experimentally manipulate a further fundamental aspect of human self-awareness, namely the spatial co-localization of the self and the body (Ehrsson 2007; Lenggenhager et al 2007). In one of these studies, Ehrsson (2007) used video technology in conjunction with head mounted displays to virtually "move" the first person visual perspective of the participants two meters behind their own bodies. Then, by applying synchronized touches to the chest of the participants and the space below the cameras (i.e. the virtual chest), the author was able to evoke a vivid perceptual illusion during which participants experienced being situated 2 meters behind their own bodies, while sensing touch originating from their virtual chest. Hence, these findings led to the demonstration that it is possible to experimentally move a person's centre of awareness outside their own body, confirming that multisensory integration is a core mechanism for the experience of a corporeal self.

It was by building on these previous findings, that we were ultimately able to develop the experimental set-up of the full-body illusion employed in the studies of this thesis, which allowed us to address the following questions: Does the mind have the capacity to attribute an entire new body to the self? What are the perceptual, cognitive and neural mechanisms that allow us to experience our bodies as part of ourselves? How come we experience the body as a unified whole rather than a set of fragmented parts?

1.3 HYPOTHESES FOR BODY OWNERSHIP

Based on the results of behavioral and neuroimaging studies of the RHI, as well as studies on multisensory neurons in primates and humans (see above) we formulated the following hypotheses:

a) The principles of the RHI should be extendable to the whole body. That is, synchronized visuo-tactile stimulation of an artificial body, which is viewed from a first person perspective, and a person’s actual body, which is out of view, should lead to illusory ownership of the artificial body.

b) Multisensory integration in body-centered reference frames is a core mechanism of body ownership.

c) The attribution of a body to oneself should be associated with activity in key multisensory brain regions such as the ventral premotor cortex and the anterior intraparietal area.

d) Multisensory integration across body segments should mediate the perceptual binding of owned body parts into a unified whole.

2 AIMS

Study I was aimed at investigating whether it is possible to induce healthy participants to experience illusory ownership of an entire artificial body. Furthermore, it aimed to identify the key perceptual processes underlying the attribution of a whole body to oneself.

Study II was specifically designed to assess the role of the visual perspective and the associated reference frame in the generation of body ownership sensations. In addition, in this study we tested whether the induction of the full-body illusion developed in Study I would be strictly dependent on the technological setup we used, or whether the illusion could also be induced in an experimental setting involving a direct view of the artificial body.

The aim of **Study III** was to shed light on the neural activity associated with the full-body ownership illusion. In addition, we investigated the mechanisms that allow the perceptual binding of owned body parts into a unified body *gestalt*.

3 METHODS

3.1 PARTICIPANTS

A total of 203 volunteers participated in the three different studies. Table 1 summarizes the details of the participants, the type of measures as well as the addressed questions for each study.

Study	N	Gender	Age mean ±SD	Measure	Question
Study I Exp. 1	32	16 f 16 m	25±6	questionnaire	Can healthy participants attribute the body of a mannequin to themselves?
Study I Exp.2	10	2 f 8 m	25±4	SCR	Can threat evoked SCR be used as an objective measure of the full-body ownership illusion?
Study I Exp.3	13	8 f 5 m	27±6.5	SCR	Is the feeling of ownership confided to the specific area of visuo-tactile stimulation?
Study I Exp.4	12	4f 8 m	29±6	SCR	Can the illusion be induced with a non-corporeal object?
Study I Exp.5	20	13 f 7 m	27±6.5	SCR	Is it possible to attribute the body of another individual to the self?
Study II Exp. 1	20	20 m	24 ± 5	questionnaire	Is the first person visual perspective essential for the full-body ownership illusion?
Study II Exp. 2	13	13 m	27 ± 4	SCR	Is the importance of the first person perspective also reflected in the threat-evoked SCR?
Study II Exp. 3	17	17 m	24 ± 4	SCR	Does the illusion depend on the technological set-up?
Study III Exp. 1	26	12 f 14 m	26 ± 6	fMRI	What is the neural activity associated with the experience of the full-body ownership illusion?
Study III Exp. 2	20	7 f 13 m	25 ± 5	fMRI	Is the neural activation associated with the illusion dependent on the visual perspective?
Study III Exp. 3	20	5 f 15 m	27 ± 7	fMRI	What is the mechanism for spread of ownership across the entire body?

Table 1. Distribution of participants across the different experiments comprising the three studies; m = male, f = female; SCR = skin conductance responses, fMRI = functional magnetic resonance imaging.

All participants were naïve to the specific purposes of the study they participated in and none of them participated in two or more experiments. The Ethical Review Board of Karolinska Institutet approved the experimental protocols and written informed consent was obtained from each participant.

3.2 PERCEPTUAL ILLUSION OF BODY SWAPPING

3.2.1 Body swapping with a mannequin

In **Study I** we created an experimental set-up in which healthy participants experienced a new body as their own body. In the first set-up, which was used in four of the experiments, we demonstrated that it is possible to achieve this illusory effect with an artificial body. For that purpose we used a life-sized mannequin (Figure 3).

To provide the participants with the first person perspective of the new body we attached two CCTV cameras (Protos IV, Vista, Wokingham, Berkshire, UK) on a custom made helmet mounted on the head of the mannequin. The two CCTV cameras were positioned so that each recorded events from the position corresponding to one of the mannequin's eyes. The spacing between the cameras was adjusted for each participant to ensure that it matched the distance between their eyes (8–10 cm). The input from the cameras was fed without any software conversion, i.e. without noticeable delay, to a set of head mounted displays (HMD) (Cybermind Visette Pro PAL, Cybermind Interactive, Maastricht, the Netherlands; Display Resolution = 640x480; true stereoscopic vision, with a wide field-of-view, diagonal field of view= 71.5°). The HMD were worn by the participants and the images from the left and right video cameras were presented on the left and right eye displays, respectively, thus providing a true stereoscopic image. Participants were asked to tilt their heads downwards as if looking down at their bodies. Hence, they saw the mannequin's body where they expected to see their own. Two identical plastic rods were used to repetitively stroke the participants' abdomen, which was out of view, in synchrony with the mannequin's abdomen, which was in full view of the participant. As a control condition, we employed asynchronous touches to the real and artificial abdomens (carefully matching the total number and length of the strokes). Each stroke was approximately 3 cm long and the number of the strokes was identical for all experimental conditions across the experiments.

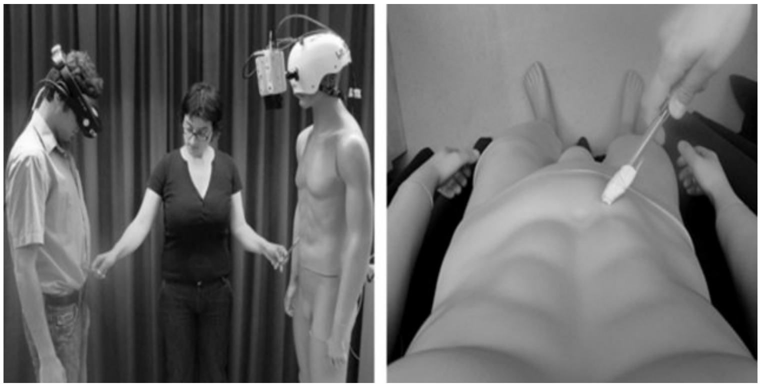

Figure 3.
Experimental set-up to induce the full body illusion (left panel).
Image presented to the participants head-mounted displays (right panel).

In **Study II** we tested the role of the visual perspective in the mechanism of body ownership. For that purpose we directly compared two experimental conditions in which the participants observed a body of a mannequin from either the first or the third person visual perspective (Figure 4). The condition in which the participants observed the body of the mannequin from the first person (egocentric) perspective was identical to the set-up described above (Figure 4a,b). However, the platform upon which the CCTV cameras were mounted was fixed on a rotating axis, which allowed the cameras to be pointed either downward to the body of the mannequin (mannequin #1, first person perspective, Figure 4a), or forward toward the body of second identical mannequin (mannequin #2, third person perspective, Figure 4c) placed opposite mannequin #1 at a distance of 75 cm. In the condition, referred to as the third person perspective, the participant was asked to position his head as if to look forward toward the body of a person standing just opposite him. In the HMDs, the participant saw the body of mannequin #2 facing him at a distance of 75 cm (Figure 4c,d). In both conditions the experimenter used two plastic rods to apply the same number of synchronized strokes on the right lateral parts of the mannequin's abdomen and the participant's abdomen.

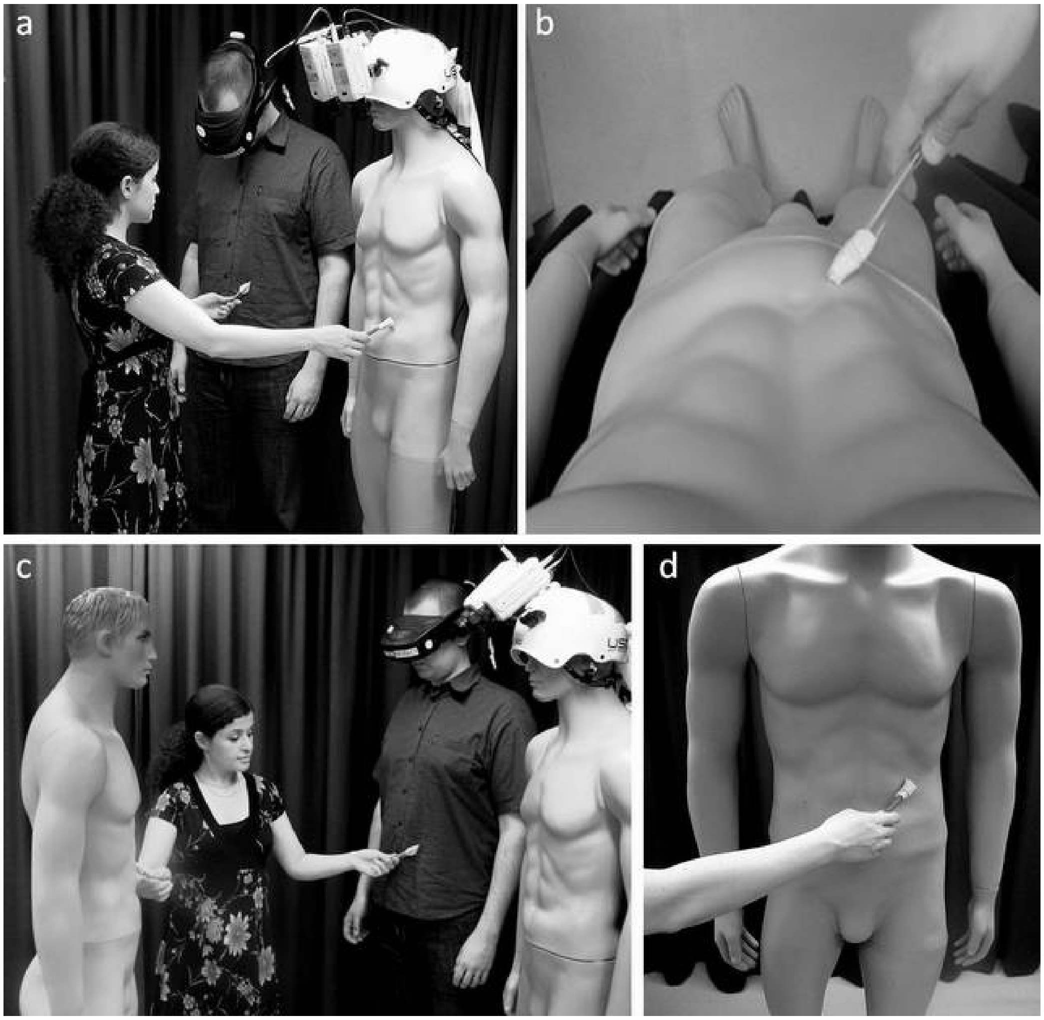

Figure 4. a,b) Experimental settings used in the second experiment to induce the illusion when participants observe the mannequin from the first person perspective. c,d) Set-up used to probe the illusion when participants observe the mannequin from the third person visual perspective.

3.2.2 Body swapping with another individual

In the fifth experiment in **Study I** we developed an experimental set-up which allowed healthy participants to experience the perceptual illusion that the body of another individual is their own body while at the same time they were interacting with their real bodies. The experimental set-up to achieve this effect was as follows:

The two CCTV cameras were attached to a custom made helmet worn by the experimenter. The cameras were positioned so that they presented the viewpoint of the experimenter. The participants stood in front of the experimenter, facing her, and wore the HMD, which were connected to the CCTV cameras on the experimenter's head. They were asked to stretch out their right arm and take hold of the experimenter's right hand, as if to shake it (Figure 5). This set-up allowed the participants to see their physical bodies from the shoulders to slightly above the knees. Hence, they could clearly recognize themselves and distinguish between their own arm and the arm of the experimenter. During the whole experiment a metronome was played out loud at 40 beats per minute. The participants and the experimenter were asked to repeatedly squeeze each other's hands for two minutes. In the illusion condition, the participant and the experimenter squeezed their hands in a synchronous manner, whereas in the control condition they squeezed each other's hands in an alternating rhythm, with the experimenter returning the squeeze in a semi-random manner.

Figure 5. Experimental set-up to induce illusory body swapping with another individual

3.2.3 Body swapping without using head-mounted displays

In **Study II** we performed an experiment which aimed to exclude the possibility that the full body ownership illusion depends on the video-technology used in the previous settings. For this, we devised an experimental set-up in which the body of the mannequin could be observed directly, either from the first or from the third person perspective.

The set-up used for the first person visual perspective condition was as follows: The participants were asked to lie on a bed tilted at 30° from the horizontal plane. The front half of the body of a shop mannequin was positioned on top of the participant so that the shoulders of the mannequin were resting on the shoulders of the participants and the feet of the mannequin were resting on a horizontal support positioned 50 cm above the feet of the participants (Figure 6a). Thus, when the participants looked down as if they were to look at their own body, they saw the body of a horizontally lying down mannequin instead (Figure 6b). The experimenter used two plastic rods to apply touches on the right lateral part of the abdomens of the mannequin and the participants, either in a synchronous or in an asynchronous mode. For the whole duration of the experiment the experimenter was out of sight, hidden behind a curtain, to prevent the participants from seeing the experimenter's hand touching their own abdomen. Thus, the only hand the participants saw was the experimenter's hand touching the abdomen of the mannequin.

The set-up used to test the illusion when the mannequin was viewed from the third person perspective was as follows: A second mannequin was placed on an identical bed as the one the participants were lying on. This bed was tilted at the same angle (approx 30°), but turned in the opposite direction, one meter to the right of the participant's bed. The participants were asked to turn their head to the right and look at the body of mannequin #2 on the other bed. A curtain was positioned over the body of mannequin #1 resting on top of the participants' body (see previous paragraph) to hide it from the participants (Figure 6c). The curtain was also occluding the experimenter, who applied synchronous or asynchronous touches to the right lateral part of the abdomens of the participants and the mannequin #2 (Figure 6d).

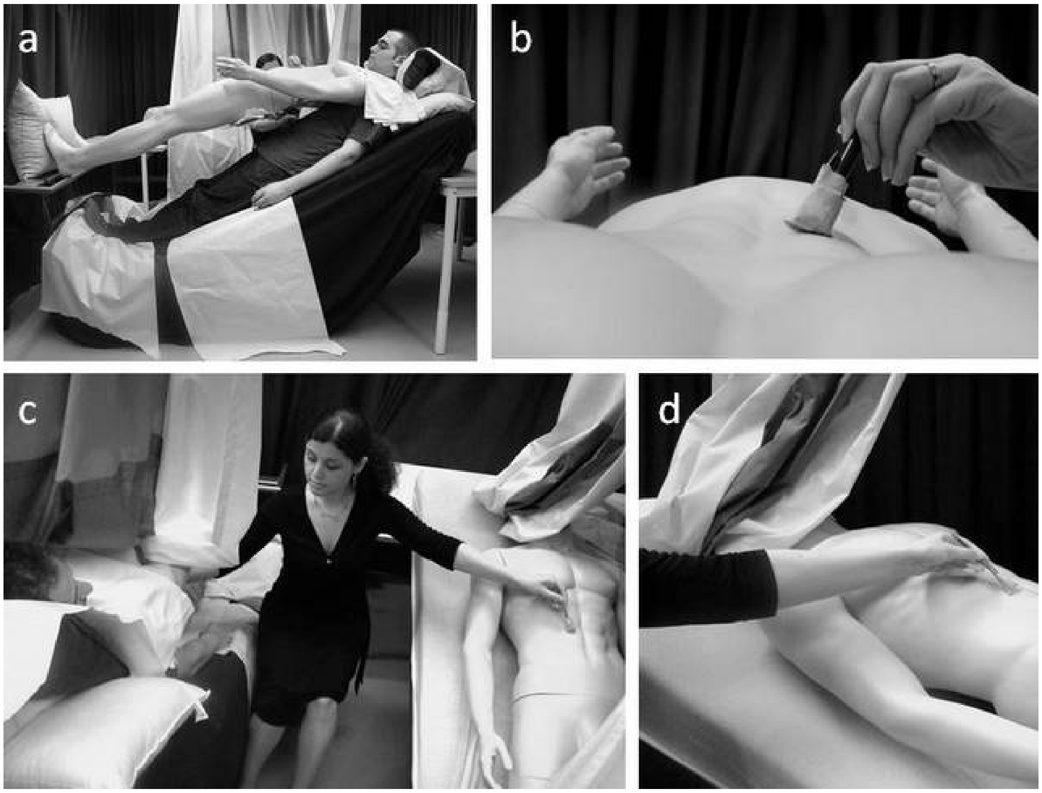

Figure 6. a) Experimental set-up to induce the full body ownership without the use of HMD. c) Set-up to probe the illusion in the third person perspective. b,d) Depict the points of view of the participants in the respective conditions.

3.2.4 Body swapping in the MR scanner

In **Study III** we created an experimental set-up which allowed us to implement the full-body illusion in a functional magnetic resonance imaging (fMRI) setting, and hence measure the brain activity of participants as they were experiencing the illusion.

During the scanning sessions, participants were lying comfortably in a supine position on the MRI table, with their head tilted at approximately 25 degrees. 3D video recordings of the visual stimuli were presented on MR-compatible head-mounted displays (HMDs; Nordic Neurolab, Bergen, Norway) positioned in front of the participants' eyes and controlled by Presentation (Version 13.1, Neurobehavioral Systems, Inc., www.neurobs.com) (Figure 7a). The 3D videos were recorded in a separate session before the fMRI experiments using a red/blue stereoscopic camera (novo Minoru, Salford, United Kingdom). Since this required separate red and blue filters to produce the stereoscopic effect, a red and a blue filter were glued in front of the left and the right display of the HMDs, respectively.

The experimenter stood on the right side of the participant and applied the touches with her index finger using small finger movements only, while standing as still as possible to minimize potential movement-induced distortions in the magnetic field (Figure 7b). Each touch stimuli corresponded to a small five-centimeter long brisk stroke. To achieve the identical number of tactile stimuli in all condition (n= 30 in each epoch) the experimenter listened to audio commands delivered via the MRI compatible headphones. The presentation of these auditory commands was digitally synchronized with the video sequences shown to the participants using Presentation software (see above). The same audio files were used when making the video recordings of the touches applied to the mannequin's body, ensuring perfect synchronization between the visual and the tactile stimuli applied to the participants' abdomen during the scans in the synchronous conditions. In the asynchronous conditions, the experimenter followed the same audio commands, however, the video recordings were delayed by one second, introducing asynchrony between the seen and felt touches. During the scans, the experimenter was blind to the visual stimulus presented to the participants, eliminating any unintentional biases in the way the touches were applied in the different conditions. The participants were instructed to look at the location on the body being stimulated and to relax.

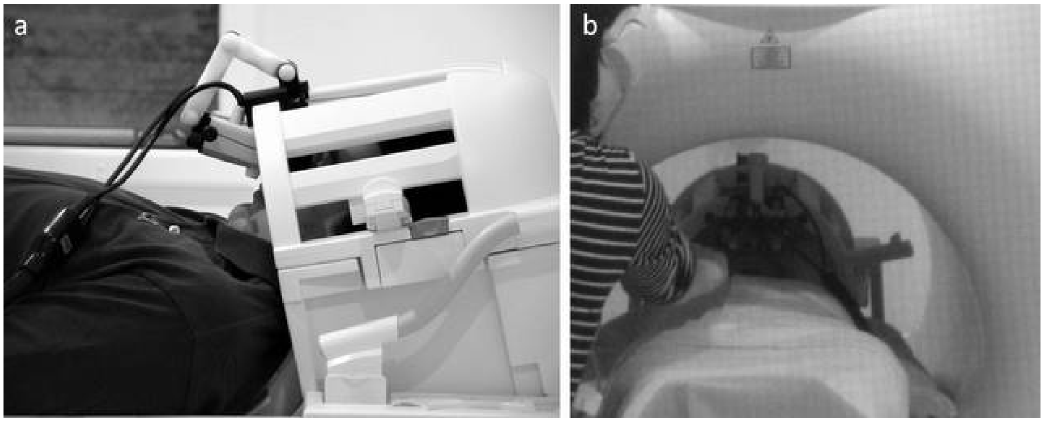

Figure 7. Experimental setup to induce the full body ownership illusion in the scanner. a) Arrangement of the scanner coil and MR-compatible HMDs b) During the entire duration of the experiment the experimenter stood near the MR scanner bed and applied tactile stimulation to the participant's body. To ensure perfect timing of the tactile stimulation with respect to the video recording audio commands were played to the experimenter via MR-compatible headphones.

3.3 BEHAVIORAL MEASURES

3.3.1 Subjective ratings of the illusion

In **Studies I** and **II** we used questionnaires to quantify the subjective experience of the participants in the different experimental conditions. The participants were subjected to either synchronous (illusion) or asynchronous (control) visuo-tactile stimulation, and were then asked to complete a questionnaire on which they had to affirm or deny different perceptual effects on a seven-point Likert scale ranging from ‘agree strongly’ (+3) to ‘disagree strongly’ (-3), with zero meaning ‘I am not sure’. Some statements were designed to capture the illusory experience of being the artificial body, and the remaining statements served as controls for suggestibility and task-compliance. The order of the statements was fully randomized for each participant.

In **Study III** we also obtained subjective ratings of the illusory experience from the participants, which were then entered in a regression analysis aimed at revealing potential correlations between the strength of the illusion and the strength of neural activation in specific brain areas. In the first two experiments of this study we requested all subjects to remain in the scanner at the end of the scanning procedure for additional 5 minutes during which they were presented with each experimental condition again. At the end of each condition, four written statements were presented on the HMDs: two statements were designed to capture the experience of the illusion, whereas the other two statements served as controls. The participants were asked to verbally report the degree of their agreement with each statement, using a rating scale from 0 to 100. These values were then used to calculate an illusion index quantifying the subjectively experienced strength of the illusion for each participant.

3.3.2 Threat-evoked electrodermal responses

The electrodermal (i.e. skin conductance) response derives from the activity of the sweat glands which in turn are controlled by the sympathetic nervous system (Malmivuo and Plonsey 1995). In the cognitive and psychological sciences there is a long standing tradition of using the measurement of electrodermal activity as an indicator of psychological or physiological arousal in response to emotional stimuli. This technique has also been specifically used to provide physiological evidence of bodily illusions (Armel and Ramachandran 2003). In this context, it has been demonstrated that there is a direct relationship between the degree of anxiety evoked by threatening an artificial body part and the strength of illusory body ownership (Ehrsson et al 2007).

In **Studies I** and **II** the skin conductance responses (SCR) were recorded in response to knife threats to the body of the mannequin (Table 1). In **Study I** we validated this test as an objective measure of the full-body illusion by comparing the evoked responses when the participants saw a knife or a spoon of a similar size to approach the body of the mannequin (Figure 8b,c). The knife and the spoon were always moved in a single ‘cutting’ motion along the horizontal axis from left to right in the field of view of the HMDs. During the movement the object was inserted slightly into the mannequin's abdomen in a small gap between the upper and lower parts of the mannequin's body. To make this possible, we placed two circular sticky patches (0.5 cm high, 1 cm diameter) between the torso and the lower part of the body of the mannequin, thereby, creating a cleft in the lower part of the abdomen of the mannequin that was not visible from the perspective of the cameras (Figure 8a) . In the fourth experiment in **Study I,** the knife was run in full contact with the non-corporeal rectangular object, but we could not induce the visual effect of cutting into it because of its flat surface (Table 1). For this particular experiment we adjusted the way that the knife threat was applied to the mannequin so that the knife was moved along touching the dummy's body, but without appearing to cut into it. The same threat motion was performed in the second and third experiments in **Study II** because those experiments contained conditions which involved seeing the mannequin from a third person visual perspective which prevented the use of a small gap between the upper and lower part of the mannequin's body (Table 1). In all SCR experiments in the two studies we took great care to move the knife or the spoon in exactly the same way from trial to trial. The exact timing of the threat events was recorded by the experimenter via a key press, and then extracted from the raw data files prior to the analysis of the data.

The SCR was identified as the peak in skin conductance occurring within a time window of 5 seconds following the onset of the threat stimuli (Figure 8d). The overall amplitude of the SCR for each threat event was measured as the difference between the minimal and maximal value of the response identified within this time window. We calculated the average of all responses including the trials where no response was apparent, thus, analyzing the magnitude of the SRC (Dawson et al 2007). Participants who did not show a reliable threat-evoked SCR ('null responders'), i.e. had zero responses in more than two-thirds of the trials, were excluded from the analysis.

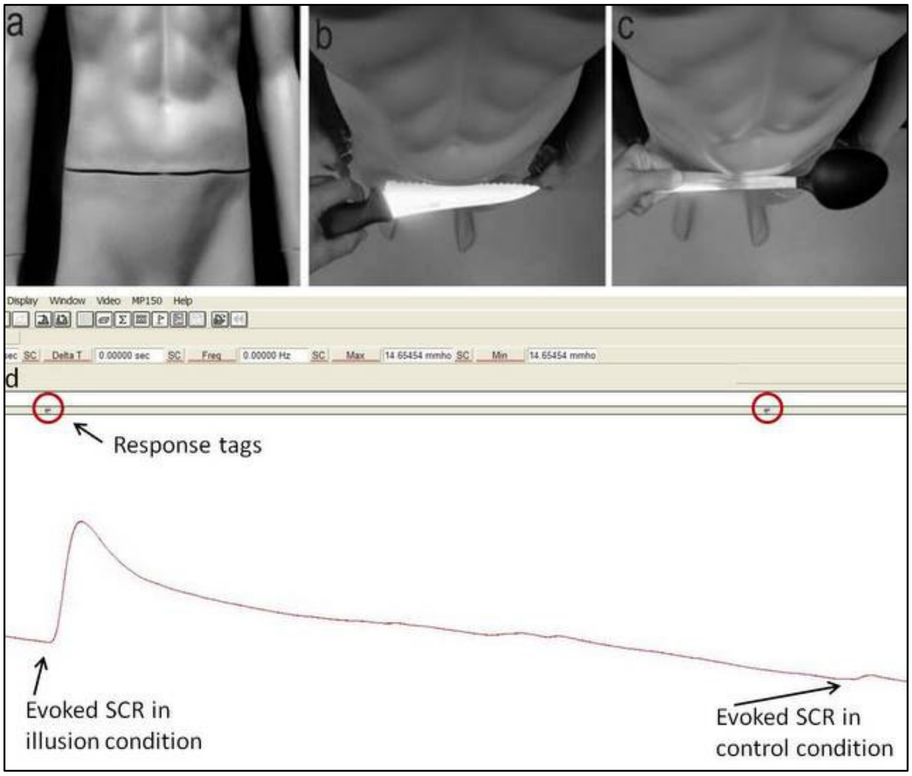

Figure 8. a-c) Threat procedures. d) Example of evoked skin conductance responses.

In all experiments and studies the skin conductance measurements were performed with a Biopac System MP150 (Goleta, USA). Two Ag/AgCl type electrodes were attached to the index and middle fingers of the participants' left hands using Signa electrode gel (Parker Laboratories, INC., New Jersey, USA). The data were registered with a Biopac System MP150 (100 samples per second) and processed with the Biopac software Acqknowledge for Windows ACK100W (Figure 8d). The participant wore the electrodes for a few minutes before starting the recording.

3.4 FUNCTIONAL MAGNETIC RESONANCE IMAGING

In **Study III** we used high field neuroimaging to investigate the neural activity associated with the experience of the full-body ownership illusion. Functional magnetic resonance imaging (fMRI) measures the changes in blood oxygenation that accompanies neural activity in the brain. Specifically, it detects the local increase in blood flow and the corresponding reduction in deoxygenated blood, by taking into account the net difference between the local blood supply and the magnitude of oxygen utilization (Buxton 2002). Oxygen is delivered to neurons by haemoglobin carried by the red blood cells in the capillaries. Haemoglobin is diamagnetic when oxygenated but paramagnetic when deoxygenated. Hence, depending on the degree of oxygenation the blood has different magnetic properties, which in turn leads to small differences in the MRI signal. Since blood oxygenation varies according to the levels of neural activity, these differences can be used to detect brain activity. This form of MRI is known as blood oxygenation level dependent (BOLD) imaging (Logothetis 2008; Ogawa et al 1990).

All three fMRI experiments of Study III were performed at the MR Center of the Radiology Unit at Karolinska Hospital, Huddinge.

3.4.1 Experimental design

In all three experiments we applied full factorial designs to address the specific questions of interest. In each experiment the condition epochs lasted 35 seconds. The conditions in experiments #1 and #2 were grouped into three blocks of four epochs, so that every condition was repeated three times within a scanning run. In experiment #3, the condition epochs were grouped in two blocks of six per scanning run. Between each condition within a block there was a short break lasting 3 seconds where the participants looked at a blank black screen and no touches were applied. After each block of four conditions (in experiments #1 and #2) or six conditions (in experiment #3), there was a 20 second baseline rest period, during which the participants were instructed to look at a black screen while no tactile stimuli were being administered. In experiments #1 and #2, each run consisted of 171 volumes and lasted for 513 seconds, and the three runs comprising the experiment were performed successively, with a break of approximately three minutes between each run. In experiment #3, each run comprised 163 volumes and lasted 489 seconds with a total of four runs with approximately three-minute long breaks between runs.

3.4.2 Acquisition and analysis of functional imaging data

All BOLD-signal changes in cortical activity were acquired at 3T (TIM Trio, Siemens, Erlangen, Germany) with a T2*-sensitive echo planar imaging pulse sequence (repetition time 3000 ms; echo time 40 ms; flip angle 90°; 47 near-axial slices; 3-mm isotropic voxel size; matrix size 58 by 76). Images were acquired using a 12-channel phased-array head coil. A high-resolution T1-weighted structural scan at 1 mm isotropic voxel size was also acquired in each subject for anatomical registration, segmentation and display. To minimize head motion, we stabilized the subject's head with the help of foam padding.

The fMRI data were analyzed with 'Statistical Parametric Mapping Software 8' (SPM8; http//:www.fil.ion.ucl.ac.uk/spm; Wellcome Department of Cognitive Neurology, London). The functional images were motion corrected, co-registered with the high-resolution structural scan, normalized to the MNI reference space and smoothed with an 8 mm FWHM Gaussian kernel. For each of the experimental conditions described above, we defined two regressors, modeling the first 10 and the subsequent 25 seconds of each stimulation period, respectively. The realignment parameters were included in the model as regressors of no interest, to account for residual head motion. Each condition was modeled as a boxcar function and convoluted with the standard SPM8 hemodynamic response function.

To accommodate inter-subject variability, the contrast images from all subjects were entered into a random effect group analysis (second level analysis). In the factorial design, we only report peaks of activation surviving the statistical threshold of $p < 0.05$, corrected for multiple comparisons. For areas where we had *a priori* hypotheses, we used the significance level that corresponded to $p < 0.05$ corrected for multiple comparisons using a small volume correction. For the rest of the brain, where we did not have such *a priori* hypotheses, we used the topological peak-FDR as implemented in SPM8.

In experiments #1 and #2, we used a second level regression model (as implemented in SPM8) to identify the brain regions in which the activity was related to the strength of the illusion as rated by the participants after the scans (using the illusion index described above). We defined a covariate corresponding to the illusion index for each participant and used the contrast images from the interaction term to search for areas in the whole brain showing a systematic relationship between illusion strength and the BOLD response.

In experiment #3 we used multivoxel pattern alanlysis (MVPA) in addition to the general linear model to examine the encoding of generalized full-body ownership. In contrast to fMRI analyses that focus on individual brain voxels, MVPA utilizes pattern-classification algorithms to unveil the information embedded in a specific pattern of brain activity across multiple voxels. The advantage of MVPA with respect to traditional single voxel analyses, is that it represents a more sensitive analytical tool which detects more subtle changes in activity (Haynes and Rees 2005; Kamitani and Tong 2005).

The functional images were pre-processed using SPM 8 in the same way as in the traditional univariate analyses described above (i.e. motion corrected, co-registered with the high-resolution structural scan, normalized to the MNI reference space and smoothed with an 8 mm FWHM Gaussian kernel). Subsequent MVPA specific pre-processing was performed with the Princeton Multi-Voxel Pattern Analysis Toolbox (www.pni.princeton.edu/mvpa).

We delineated the region of interest for voxels carrying illusion-related information using locally-multivariate Monte Carlo brain mapping (Björnsdotter et al 2011). A linear support vector machine (in the LIBSVM implementation; http://www.csie.ntu.edu.tw/wcjlin/libsvm/, with fixed regularization parameter C = 1) was used to model the conditions, and the proportion of correctly decoded trials (in an independent test dataset) was used to indicate the multivariate information content. The search volume size was set to 4mm.

4 RESULTS AND SHORT DISCUSSION

4.1 STUDY I

In this study we addressed the question of whether healthy individuals can be induced the illusory sensation of owning a new (artificial or real) body. In addition, we investigated the perceptual and cognitive mechanism underlying the process of attributing a body to oneself. By drawing inspiration from previous research on the rubber hand illusion (see introduction), we created a novel experimental set-up in which participants viewed a whole body from a first person perspective, while being subjected to synchronous visuo-tactile stimulation through stroking. We quantified the participants' subjective experience of the illusion through questionnaires, and found that irrespectively of their gender about 70% of them affirmed the illusory sensation of perceiving the body of a male life-size mannequin as their own (Experiment 1, Table 1). We then used threat-evoked skin conductance responses to demonstrate that this illusion of ownership is not confined to the specific area of sensory stimulation, but that it spreads encompassing the whole body (Experiment 3, Table 1). In addition, we found that the illusion breaks down when the tactile and visual inputs (coming from the participants' and mannequin's body respectively) are temporally incongruent (Experiment 1, 2, and 3), or when the body is replaced with a rectangular object that does not have humanoid shape (Experiment 4, Table 1).

Remarkably, when we replaced the body of the mannequin with the body of another individual we found that naïve participants could perceive strong ownership of this other body even when they were interacting with their 'old' real bodies (Experiment 5, Table 1). This illusory effect was maintained as long as the convergent visual, motor and tactile inputs coming from the new body were matching those from the real body, even when the real body was in full view of the participants. Once again, the gender or the specific visual features of the new body did not affect the strength of the body ownership illusion.

Taken together, these results demonstrate that it is possible to 'move' the human centre of awareness from one body to another. In addition, they suggest a set of perceptual rules that constrain the perceptual experience of body ownership and which correspond to the mechanisms of multisensory integration.

4.2 STUDY II

In the previous study we did not directly contrast the first person and third person visual perspectives, and therefore did not directly examine the role of the egocentric reference frame for the generation of the full-body illusion. In spatial cognition one differentiates between the first and the third person visual perspectives (Vogeley and Fink 2003), which in turn are related to the concept of ego- vs. allocentric reference frames (Burgess 2006; Klatzky 1998). An egocentric reference frame is a coordinate system centered on the body, and is considered to be important for functions related to perception and action performance (Fogassi et al 1992; Graziano and Gross 1998). In contrast, an allocentric reference frame corresponds to world coordinates centered on a reference point in extrapersonal space. This coordinate system is considered important for spatial cognitive functions such as determining one's location with respect to environmental landmarks, spatial navigation, and spatial memory (Burgess 2006; Maguire et al 1998).

The concept of the two reference frames also relates closely to the distinction between multisensory neuronal populations which respond to stimuli that are either close or far from the body (Rizzolatti et al 1981). Hence, it has direct bearings on the process of multisensory integration in peripersonal space (see Introduction).

The results from Study I, together with results from previous research on the rubber hand illusion (Makin et al 2008), led us to the hypothesis that the core of the process of attributing a body (part) to oneself is the mechanism of multisensory integration in peripersonal space.

In **Study II,** we therefore directly tested the prediction that the multisensory processes giving rise to the full-body illusion operate in body-centered reference frames. To that end we compared two experimental conditions in which the tactile stimulation and the body of the mannequin could be perceived either from a first person perspective, i.e. in near-personal space (see Study I) or from a third person perspective, i.e. in a location opposite the participant in far extrapersonal space.

Our results revealed that the perception of the full body ownership illusion is only possible when the converging visuo-tactile input triggering the illusion is perceived from a first person perspective in near personal space. Hence, our results provide strong behavioral evidence that the attribution of a body to oneself is directly linked to the mechanism of multisensory integration in body-centered coordinate system.

In an additional experiment, we confirmed those results in a set-up in which the body of the mannequin was viewed with direct vision, hence demonstrating that the body ownership illusion is a genuine perceptual experience and cannot be explained simply by the use of head mounted displays and video technology.

4.3 STUDY III

In this study we investigated the neural underpinnings of the full-body ownership illusion reported in **Studies I** and **II**. In addition, we addressed the mechanism which underlies the spread of ownership from the site of stimulation to the rest of the body (see Study I) and allows the perceptual binding of owned body parts into a unified corporeal self. To that end we performed three independent fMRI experiments which addressed specific aspects of our hypotheses.

In the first experiment we sought to identify the neural activations related to the perception of a body as belonging to oneself. When participants viewed the body of a life size mannequin from a first person perspective while being subjected to synchronous visuo-tactile stimulation, we found a significant increase in activity in the ventral portions of the bilateral premotor areas and the left anterior intraparietal sulcus compared to conditions in which the mannequin's body was replaced by a wooden object of similar size or when the visuo-tactile stimulation was asynchronous.

The significant activity in those multisensory areas is in line with results from previous neuroimgaing studies on limb ownership based on the rubber hand illusion (Ehrsson et al 2005; Ehrsson et al 2004) and provides compelling evidence that the self-attribution of a body (part) is mediated via integration of visual, tactile, and proprioceptive information by neuronal populations in the ventral premotor and intraparietal cortices.

Following the results of **Study II** (see above), we predicted that this body ownership related brain activity would be significant only when participants perceive the convergent visuo-tactile stimulation driving the experience from a first person, i.e. in near personal space. To test this hypothesis we conducted a second fMRI experiment in which a new group of naïve participants perceived the mannequin's body either from the first person or the third person perspective. In strong agreement with our prediction we found significant activity in the left ventral premotor area and the left anterior intraparietal sulcus only when the body of the mannequin was perceived from the first person perspective in combination with congruent visuo-tactile input. It is important to note that in this condition we also observed activation in the left putamen which corresponded to a non-significant activity in this area observed in the first fMRI experiment. Studies both in humans (Gentile et al 2011) and in non-human primates (Graziano and Gross 1993) have identified the putamen as an area containing body-centered multisensory neurons.

Hence, both independent fMRI experiments provided converging evidence that the attribution of a body to oneself is related to neuronal computations in the ventral portion of the premotor area, the intraparietal sulcus and the putamen all of which integrate multisensory input in body-centered reference frames (Figure 9a-c). Moreover, the level of activity in the premotor area in both experiments was significantly correlated with the strength of the subjective full-body ownership experience as measured by the illusion index (see methods) suggesting a possible role of this area in the conscious perception of the body as part of the self (Figure 9d).

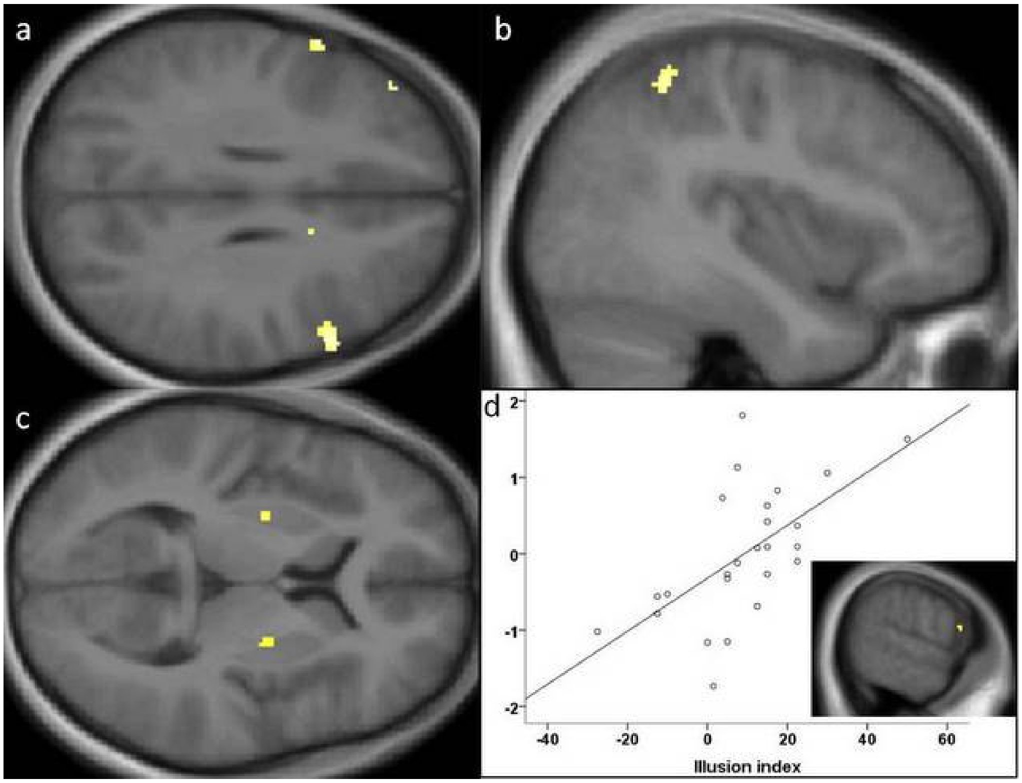

Figure 9. Examples of activity in a) bilateral premotor cortex b) left intraparietal sulcus c) left putamen. d) Activity in the ventral premtor cortex was significantly correlated with the subjective strength of the experienced full-body ownership illusion as measured by the illusion index. Activation maps correspond to the interaction term in the factorial design in Study III (p set to 0.001 for display purpose), superimposed on a mean anatomical image.

In both experiments, however, the full-body ownership illusion was triggered by stimulation to the abdomen, i.e. a single body part. Hence, the mechanism underlying the spread of ownership so as to encompass the whole body as behaviorally observed in **Study I** remained unclear. Electrophysiological studies in non-human primates have shown that some multisensory neurons located in the premotor and intraparietal areas have visuosomatic receptive fields extending across several body segments (Duhamel et al 1998; Fogassi et al 1996; Graziano and Gandhi 2000; Rizzolatti et al 1981) sometimes even encompassing the entire body (Graziano and Gandhi 2000).

To directly test the hypothesis that multisensory integration across body segments mediates the perceptual binding of owned body parts into a unified whole, we conducted a third fMRI experiment. We found that when participants experienced stimulation to an intact body that was perceived as a whole, as opposed to a single detached arm, there was a significant increase in activation in the left ventral premotor area, the left intraparietal sulcus and the left putamen. Furthermore, we found voxels in the ventral premotor and the anterior intraparietal areas which were active when the full-body ownership illusion was triggered by stimulation both on the hand and on the abdomen. A formal conjunction analysis revealed that only the voxels in the left ventral premotor area survived the statistical threshold for multiple comparisons. To exclude the possibility that this finding reflects mixed neuronal population in those voxels which have receptive fields restricted to individual body parts, we performed a multivoxel pattern analysis which is sensitive to fain-grained spatial patterns and subvoxel information (Haynes and Rees 2005; Kamitani and Tong 2005). We found that the same voxels in the ventral premotor area decode full-body ownership when it is triggered by congruent visuo-tactile stimulation to the hand and to the abdomen. Importantly, those voxels did not decode the illusion when the perceived visuo-tactile stimulation was coming from a single detached arm. Taken together, these results suggest that the ventral premotor area contains neuronal populations which mediate the spread of ownership to the whole body.

Further research will be needed to understand the specific functional role of the different areas identified in our experiments with respect to the precise mechanism of the perceptual origin and experience of the corporeal self.

4.4 UNPUBLISHED DATA (STUDY III)

In the first two fMRI experiments in **Study III** we found consistent activity in the left lateral occipital cortex (LOC) when we performed a conjunction analysis of the main effects in the respective factorial designs (Figure 10). The coordinates of the peak activation in LOC were in a location that most likely corresponds to a sub-region of this cortex called the extrastriate body area (EBA), which is selectively activated by visual perception of bodies and body-parts (Downing et al 2001; Kontaris et al 2009; Peelen and Downing 2005, 2007). Our results suggest that this part of the visual cortex might contribute to the visual self-recognition of a body. The activity in this region was enhanced during the illusion, in particular when synchronous visuo-tactile stimulation was applied to the mannequin's body, but only when it was observed from the first person perspective. This effect is most likely mediated via anatomical feed-back connections from posterior parietal areas involved in the basic mechanisms underlying the illusion (Lewis and Van Essen 2000). It is important to note that the consistent EBA activity we observed the two experiments of our study, was restricted to the left EBA. In apparent contrast with this finding, a previous study found that the right EBA seems to selectively respond to images of the own body, as opposed to images of other individuals or scrambled body images (Vocks et al 2010). However, in this study the various body images were presented on a computer screen, that is the participants viewed them from a third-person perspective.

Consistent with this, another study showed that the right EBA selectively responds to visual images of bodies presented from an 'allocentric' viewpoint (i.e. third person perspective) (Saxe et al 2006). The left EBA in contrast did not seem to distinguish between images viewed from a first or third person visual perspectives. What distinguishes our study from that of Saxe at al. (2006) though, is that our participants did not merely view a body from a first person perspective, but they were in fact experiencing ownership over that body. Hence, our study adds to our current understanding of the properties of the EBA, by showing that its activity can be specifically modulated by ownership sensations.

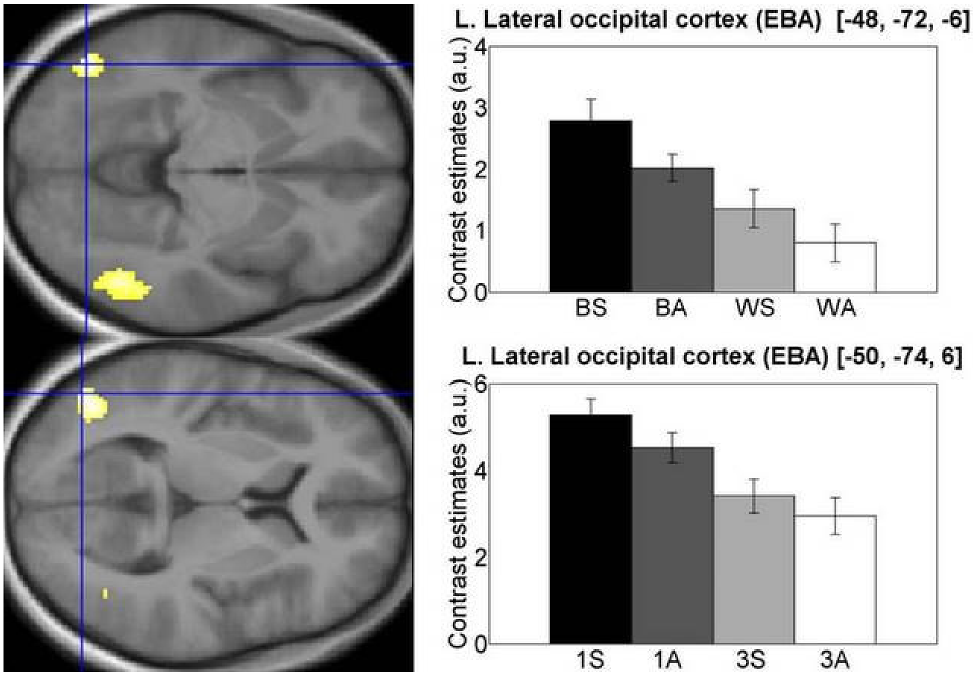

Figure 10. Activity in the left lateral occipital cortex (extrastriate body area) in fMRI experiment #1 (panel above) and fMRI experiment #2 (panel below). Activation maps correspond to the conjunction analysis in the factorial designs (p value set to 0,001 for display purpose), superimposed on a mean anatomical image. The plots represent the contrast estimates (beta parameters of the general linear model) for the significant peaks of activation.

5 GENERAL DISCUSSION

> *„Nature also teaches me by the sensations of pain, hunger, thirst, etc. that I am not only lodged in my body as a pilot in a vessel, but that I am very closely united to it, and so to speak so intermingled with it that I seem to compose with it one whole"*
>
> *Rene Descartes, Meditations VI*

5.1 MULTISENSORY INTEGRATION AND BODY OWNERSHIP

The results of the three studies presented in this thesis provide converging evidence in support of the hypothesis that experiencing a body as belonging to oneself is primarily driven by multisensory integration. This neural mechanism relies on the properties of population of neurons called multisensory neurons, that integrate the input from multiple sensory modalities, i.e. vision, proprioception, and touch (Graziano and Gross 1994; Rizzolatti et al 1981) (see Introduction). The firing of multisensory neurons is in turn modulated by the spatial properties of their receptive fields. For instance, they fire not only when their tactile receptors are activated, but also when an object approaches their tactile receptive fields (typically within a distance of up to 30 cm) (Graziano and Gross 1994; Rizzolatti et al 1997; Rizzolatti et al 1981). This space around the body in which this visuo-tactile integration occurs is referred to as peripersonal space. It is particularly pronounced around the hands and head, and has been proposed to be crucial for multisensory perception as well as goal directed reaching and defending behavior (Fogassi et al 1992; Graziano and Gross 1998).

In the context of our behavioural studies employing a full-body illusion (**Study I and II**), we first showed how the perceptual 'rules' underlying full-body ownership are linked to the mechanism of multisensory integration. Specifically, we demonstrated that the sensation of full-body ownership arises only when (i) the visual, proprioceptive and tactile input coming from the body is spatially and temporally congruent, (ii) when the converging multimodal input is perceived from a first-person perspective, and (iii) when it occurs in peripersonal space. Moreover, we showed that all else remaining equal the sensation of ownership does not arise if the body from which the stimulation is perceived is replaced by a non-corporeal object (i.e. a wooden block of similar dimensions). Hence, multisensory integration mechanisms seem to specifically drive the experience of a corporeal self.

By implementing the full-body illusion in a neuroimaging setting (**Study III**), we were then able to confirm our multisensory integration hypothesis at a neural level. That is, we showed that the sensation of body ownership is associated with a significant increase in activity in key multisensory brain areas which integrate visual, somatic and proprioceptive signals, i.e. the ventral portion of the premotor cortex, the anterior part of the intraparietal sulcus and the putamen (Avillac et al 2007; Avillac et al 2005; Bremmer et al 2001; Duhamel et al 1998; Fogassi et al 1996; Graziano and Gandhi 2000; Graziano and Gross 1993; Graziano et al 1997; Rizzolatti et al 1981). Electrophysiological studies in non-human primates have shown that all these areas contain multisensory neurons, and that they receive anatomical projections from early visual and somatosensory areas in the occipital and anterior parietal (Pandya and Kuypers 1969; Pearson and Powell 1985; Rizzolatti et al 1998; Vogt and Pandya 1978). Even more importantly with regard to our findings, recent neuroimaging studies have shown that the human premotor cortex, intraparietal areas, and putamen also perform integration of visual and somatosensory signals in peripersonal space, akin to that described in the macaque brain (Brozzoli et al 2011; Gentile et al 2011; Makin et al 2007).

Of particular interest were the results of the first two fMRI experiments of **Study III**, which both showed that the strength of the subjective experience of ownership of the mannequin's body was significantly correlated with activity in the left ventral premotor cortex. In our third fMRI experiment we then explored the activation patterns of this area in even more detail with multivoxel pattern analysis. Intriguingly, we found that a specific sub-region was active regardless of the exact location of the multisensory input (i.e. the hand or the trunk), whereas other sub-regions selectively responded to the stimulation of individual body parts (i.e. only the hand or only the trunk). In other words, there seem to be some neural populations in the ventral premotor cortex with small receptive fields encompassing individual body segments, and others with larger receptive fields encompassing multiple body segments or possibly even the whole body. Although the spatial resolution of the BOLD signal does not enable one to draw any definite conclusions in regard to the receptive field size of individual neurons in humans, this interpretation is supported by electrophysiological studies in monkeys, which have in fact demonstrated the existence of multisensory neurons with such differential receptive field sizes (Fogassi et al 1996; Graziano 1999; Graziano et al 1997; Rizzolatti et al 1981). It is the interplay of these neurons that can be hypothesized to underlie the unified perception of a whole body *gestalt*, which is more than a mere assembly of fragmented parts. A possible neurophysiological mechanism at play in this context could be mediated via horizontal connections between the different sub-regions of the ventral premotor cortex. Specifically, neuronal population with small and selective receptive fields could signal the exact location of the sensory input from the body, whereas activity of neurons with large receptive fields could signal the sensation that this location "belongs" to a unified whole body.

Albeit speculative, these interpretations can be supported by the following results from the third experiment of our fMRI study: Firstly, when participants observed a detached arm that was not part of an intact body, the activity in both the ventral premotor cortex and the intraparietal suclus significantly decreased relative to the condition in which the participants viewed synchronized visuo-tactile stimulation on a whole intact body. Secondly, the activity of sub-regions of the ventral premotor cortex that was selectively driven by stimulation of the trunk, was modulated by stimulation of the hand only when the hand was perceived as belonging to a unified intact body. It is particularly interesting that the perception of a unified full-body gestalt seems to be associated with neural activity in the ventral portion of the premotor cortex, as activation of this area is also associated with consciously experiencing a body as belonging to oneself as indicated by the significant correlation of the activity in this region and the subjectively rated strength of the full-body illusion in experiments #1 and #2 in Study III. However, further research is needed to pinpoint the respective roles played by the ventral premotor cortex, the intraparietal sulcus and the putamen (as well as the interplay between these regions) in the generation of full-body ownership sensations.

In sum, the studies of this thesis provide compelling evidence for the fact that multisensory integration, driven by neural activity in brain areas that integrate signals from different sensory modalities for the control of sensory-guided actions in body-part-centered reference frames (Fogassi et al 1992; Graziano and Gross 1998), is the core mechanism underlying the perception of a corporeal self.

5.2 IS THERE AN EXTENDED NEURAL NETWORK OF BODY OWNERSHIP?

The results of **Study III** showed that the sensation of body ownership is associated with the activity of a cortical network involving multiple multisensory brain areas. Neural populations in these areas, however, code for other perceptual, cognitive and behavioral functions as well (Ehrsson et al 2000; Halsband and Freund 1990; Halsband and Passingham 1982; Kurata and Hoffman 1994; Mountcastle et al 1975; Murata et al 2000; Pardo-Vazquez et al 2008, 2009; Passingham 1993; Romo et al 2004; Sakata et al 1992; Sakata et al 1995; Taira et al 1990; Weinrich et al 1984; Wise 1985). Hence, there does not appear to be a selective neural network solely devoted to the experience of a corporeal self as such, as it has been recently suggested (Blanke and Metzinger 2009). Naturally, two important questions arise: First, is this fronto-parietal network the sole contributor for the conscious perception of the corporeal self? Second, exactly how does the activity within this distributed cortical network end up generating a conscious sensation of ‘belonging’ to a body? In section 7 of this thesis I will propose a personal, if speculative, attempt of answering the second question.

An important clue for the answer to the first question comes from case studies of patients with somatoparaphrenia, a neurological condition that specifically affects what can be defined as ‘qualia’ (i.e. subjective conscious experience) of body ownership. The clinical picture of somatoparaphrenia is complex, as the condition has been found to be associated with lesions in a large variety of brain regions including subcortical structures and white matter tracts (see Introduction). Interestingly, a recent study pointed out how in most cases the white matter tract lesions seem to specifically affect the connections between the ventral premotor cortex and other brain regions (Zeller et al 2011). Thus, it seems likely that a distributed cortical network in which a central role is played by the ventral premotor cortex is crucial for the perception of the corporeal self, and that a disruption of this network leads to disturbed body ownership.

Hence, it seems plausible to assume that the mechanism of multisensory integration, identified in the studies outlined above, plays a central role in a larger distributed network which jointly brings about the intimate sensation of the corporeal self. What could be the other constituents of this network?

The first person visual perspective

One important property that distinguishes the own body from all other objects is the unique and invariable visual perspective we have of it. Most objects in our environment can be observed from different angles and perspectives, but we can never see the back of our own body, the wrinkles around our eyes, or the whitening roots of our hair without the use of mirrors, photographs or video recordings of our bodily self. Indeed, the results of **Study II** outline the crucial role of the first person perspective for the attribution of a body to oneself. Apart from its importance in defining the egocentric reference frame in the mechanism of multisensory integration in peripersonal space, the first person perspective provides us with a unique visual image of our body, which is important in its own right. In fact, in **Study III** we found that viewing the body of the mannequin from a first person perspective in conjunction with congruent tactile stimulation, was associated with increased activity in the left extrastriate body area. This area is a higher order visual area located in the lateral occipital cortex, which is specialized in the visual perception and discrimination of bodies (Downing et al 2001; Kontaris et al 2009; Peelen and Downing 2007). Previous studies had already shown that the activity of the (EBA) can be modulated by the visual perspective of a seen body (Saxe et al 2006; Vocks et al 2010), but our findings further build on this notion by demonstrating that this region is modulated by the sensation of ownership of a body. Furthermore, since the EBA is anatomically connected with parietal and premotor areas (Lewis and Van Essen 2000), it is also likely to be one of the constituents of the distributed neural network generating the perceptual sensation of body ownership.

The somatosensory input

A further unique attribute of our own body is the fact that it is the only source of 'first hand' sensory experiences. Our own body is the only one through which we can sense physical touch, pressure or pain. Interestingly however, in none of our neuroimaging experiments we observed any correlation between the strength of body ownership sensations and activation in primary somatosensory areas. One possible explanation could be that in all experimental conditions participants experienced the exact same sensory stimulation to their actual bodies, as well as constant congruent proprioceptive input. Hence, it is feasible to assume that the power of the interaction contrast between the different experimental conditions in our experiments was not sufficient to drive a significant modulation in the somatosensory system.

Nevertheless, it is important to acknowledge that the sense of proprioception (which is also mediated by the somatosensory system) provides us with unique information about the posture and spatial configuration of our own body. Hence, it undoubtedly represents a crucial factor when it comes to attributing a body to ourselves. In fact, the utter importance of this sense has been outlined in a neurological case report of a patient suffering from complete loss of her sense of proprioception resulting in an unsettling sense of "disembodiment" [(Sacks 1998), p. 49]. Similarly, in a recent experimental study, it has been found that following anesthetic block healthy participants experienced illusory finger ownership based entirely on congruent visual and proprioceptive input (Walsh et al 2011). Thus, continuous afferent proprioceptive input is likely to be necessary for the perception of body ownership. However, the results in our study suggest that the conscious experience thereof does not necessary rely on modulations of activity in primary somatosensory cortices. Nevertheless, it is important to emphasize that the key multisensory brain areas which were active during the full-body ownership illusion integrate visual, tactile and proprioceptive input in body centered reference frames. As it will be discussed in greater detail below, however, activity modulations in primary and secondary somatosensory cortices have been proposed as a neural mechanism for self-other differentiation (Avikainen et al 2002; Saxe et al 2006).

Agency

An important characteristic of the own body is that its motor output generally corresponds to the intentioned motor behavior, i.e. sense of agency (Jeannerod 2003, 2007), or to the sensory-motor predictions in case of voluntarily motor actions (Blakemore et al 1998; Wolpert et al 1995; Wolpert and Flanagan 2001). The complex interplay between the sense of agency and the perception of body ownership has been a subject of extensive experimental investigation (de Vignemont and Fourneret 2004; Kalckert and Ehrsson under review; Tsakiris et al 2010b; Tsakiris et al 2007b; van den Bos and Jeannerod 2002). It appears that the two phenomena are introspectively linked (Longo et al 2008), and that both contribute to cognitive self-recognition (van den Bos and Jeannerod 2002). However, they seem to be dissociable when their characteristics and effects are carefully compared in behavioral (Kalckert and Ehrsson under review) and neuroimaging (Tsakiris et al 2010b) experiments. Supportive evidence for the dissociation between the two phenomena comes from the Alien hand syndrome, in which the affected patients' hand does not obey their will and instead appears to have a mind of its own (Assal et al 2007; Della et al 1994; Goldberg et al 1981). Despite the autonomous behavior of the affected hand, and the inability to control its movement, many patients nevertheless retain a sense of ownership over it (Marcel 2003). Thus, it seems that on both a behavioral as well as a neural level, the presence of a sense of agency is not essential for the experience of body ownership.

In all but one of our experiments the full-body illusion was induced solely through visuo-tactile synchronization, with the participants remaining passive throughout the experimental procedure. Only in experiment #5 of **Study I**, in which the participants experienced illusory body swapping with the experimenter, the synchronous visuo-tactile stimulation was a accompanied by concomitant synchronized motor behavior (i.e. hand clasping). Hence, from the results in our studies it is clear that full-body ownership can be elicited without voluntary action, i.e. purely by multisensory correlations, and that it can be maintained during voluntary action as long as the seen and felt movement are spatially and temporally congruent. In addition, and of particular interest, a large percentage of participants across all three studies spontaneously remarked that as they experienced illusory ownership over the artificial body, they were also expecting it to obey their potential intention to move. Therefore, it seems to be the case that experiencing ownership over a body is a prerequisite for experiencing agency over it, but that agency in itself is not enough to drive ownership sensations.

Me and my body are spatially co-localized

The sense of our own body is intimately linked to the perception that we are constant 'inhabitants' of it. That is, generally speaking our body and our centre of awareness are spatially co-localized. This union of the self and the body can however be interrupted in individuals who have spontaneous or evoked out of body experiences (Blackmore 1982; Blanke et al 2004; Blanke et al 2002; Brugger et al 2006; Devinsky et al 1989; Grusser and Landis 1991; Irwin 1985).

Studies of epileptic patients involving electrophysiological stimulation during pre-surgical localization of seizure onset, have shown that bilateral stimulation of the temporo-parietal junction (TPJ), and particularly the superior temporal gyrus, elicits vivid experiences of being outside one's own body (Blanke et al 2004). In addition, as mentioned in the introduction such out of body experiences can also be induced experimentally in healthy individuals with the use of video technology and concomitant manipulation of visuo-tactile input observed either from the first person visual perspective (Ehrsson 2007), or from the third person visual perspective (Lenggenhager et al 2007). A neuroimaging study which used the experimental protocol developed by Lenggenhager et al (2007) has found the experimentally induced dissociation between the localization of the self and the body to be associated with a bilateral change in activity in the TPJ, again most pronounced in the superior temporal gyrus (Ionta et al 2011). Hence, it seems like the TPJ plays an important role when it comes to detect incongruencies between the localization of the self and the body, which is in line with its known role of detecting a range of contradicting or surprising sensory inputs (Astafiev et al 2006; Corbetta and Shulman 2002; Kincade et al 2005; Shulman et al 2009). In fact, in the second fMRI experiment of Study III we observed a significant increase of activation within the left TPJ reflecting a main effect of asynchronous visuo-tactile stimulation, regardless of the visual perspective from which the body of the mannequin was perceived. In addition, we did not observe any significant increase in activation in this region in any of the conditions in which the participants perceived ownership of the mannequin's body. It can be, thus, speculated that this region plays an indirect role in the perception of body ownership as it primarily signals salient incongruencies which need to be attended to (Corbetta and Shulman 2002). Therefore, it might not be surprising that epileptic or direct electrical stimulation in this region of the TPJ leads to the perceptual separation between the experienced center of awareness and the body, i.e. to an out of body experience.

However, TPJ and specifically the superior temporal sulcus have been shown to play an important role also in social cognition and theory of mind (Dodell-Feder et al 2011; Frith and Frith 2006; Samson et al 2004). These and related concepts of the functionality of this region would be discussed in greater detail further below in the section of the discussion which deals with a possible wide distributed 'self-other' brain network and its potential role in the mechanisms giving rise to the qualia of the corporeal self.

Additional possible components in the extended brain network contributing to the perception of body ownership

In addition to purely sensory-motor information, there are other important cognitive and physiological aspects that can be assumed to significantly contribute to the sensation of bodily self. A detailed discussion of all these potential aspects goes beyond the scope of the current discussion, but I would nevertheless like to just briefly mention at least a few of them:

a) *Autobiographical (episodic) memory*, which is linked to a self-memory system that provides information on what the self is, what the self was, and what the self can be (Conway 2005). This information is categorized into three broad areas: lifetime periods, general events, and event-specific knowledge (Conway and Pleydell-Pearce 2000). In a nutshell, it is likely that the autobiographical memory system provides longitudinal information about the own body appearance, its sensory-motor characteristics and overall knowledge of its development.

b) *Interoception*, which provides information on internal bodily states. According to Craig (2003) the primary function of the interoceptive system is to provide welldiscriminable feelings from the body that include pain, temperature, itch, sensual touch, muscular and visceral sensations, vasomotor activity, hunger, thirst, and 'air hunger'(Craig 2003). To quote the author: "…a metarepresentation of the primary interoceptive activity is engendered in the right anterior insula, which seems to provide the basis for the subjective image of the material self as a feeling (sentient) entity, that is, emotional awareness". It is worth mentioning, that in a positron emission tomography study employing the RHI, activity in the right posterior insula has been observed in correlation with the perceived proprioceptive drift towards the rubber hand (Tsakiris et al 2007a). In addition, it has been shown that people with low interoceptive sensibility as measured with heartbeat monitoring task experience a strong perceptual illusion of ownership in the rubber hand illusion (Tsakiris et al 2011). While undoubtedly intriguing, further studies are needed to understand the exact implications of these findings.

c) *Attention*, which is linked to the more general sense of self-awareness. The relationship between attention and awareness has been the focus of a wealth of past research studies (Dehaene et al 2006; Kentridge et al 2004; Koch and Tsuchiya 2007; Naccache et al 2002). Of most relevance in the current context is research on hemispatial neglect. This neurological condition occurs most commonly after a right hemisphere damage and is characterized by the loss of ability to process stimuli in the contralesional side of space including the own body (Brain 1941; Critchley 1953). Lesions both in temporo-parietal and frontal lobes have been reported in clinical populations with this syndrome (Karnath et al 2001; Ptak and Schnider 2010; Vallar and Perani 1986).

In sum, the conscious experience of body ownership appears to be driven by a distributed neural network, with particular emphasis on higher order multisensory areas that integrate visual, tactile and proprioceptive input in body-centered reference frames. Further experimental and clinical research will be essential to shed further light on the nature of the interconnections between the different constituents in this network, and their relation to different aspects of bodily self-consciousness and neurological disturbances thereof. Still open, in addition, is a question of more philosophical nature: How does the conscious perception of bodily 'mineness' (a term first coined by Heidegger in *Being and Time*, 1927, to denote the own being) arise? In other words, how does the activity within this wide spread brain network bring about the qualia of the bodily self? Further below in section 7 of this thesis I will address a series of aspects that need to be considered in this regard, and propose a personal, if speculative, attempt of answering this question.

5.3 DO I NEED A BODY TO KNOW WHO I AM?

The results of the studies presented in this thesis provide an affirmative answer to this question, as they show that we need converging sensory input from our body to construct our corporeal self. However, the current work opens up another intriguing question: Do I need *my* body to know who I am? Paradoxically, the answer to this second question seems to be 'no'. What I am referring to here with the term 'my' is our actual body, the one that we experienced as 'ours' since our birth. As the results of

Study I and Study II clearly demonstrated, only a few seconds of congruent visuo-tactile stimulation experienced from a first person perspective seem to be sufficient to induce healthy participants to experience the body of a mannequin or the body of another individual as their own, regardless of striking differences in gender, visual characteristics, or skin tone. In addition, the results of Study III showed that the visuo-tactile stimulation leading to the perception of an artificial body as belonging to oneself results in activation in similar multisensory brain areas as the visuo-tactile stimulation of the own body (Brozzoli et al 2011; Gentile et al 2011). Based on these findings, we can conclude that the body image seems to be remarkably malleable, and that major changes in the visual appearance of our own body do not lead to a loss of self-identity. From an evolutionary perspective, this remarkable flexibility can be assumed to have developed in order to allow for a perpetually experienced integrity of an aging, growing and ever changing body appearance.

6 FUTURE DIRECTIONS

Work in progress

The studies conducted during the course of this work represent only an initial step towards the understanding of the neural underpinnings of the corporeal self. Current work in progress is devoted to more detailed investigations of the characteristics of the receptive fields of multisensory neurons in the three key regions (PMv, IPS, and putamen) that we have found to be associated with the full-body ownership illusion. Specifically, we aim to shed further light on the exact neural mechanisms underlying the perception of a whole unified body, as opposed to a mere collection of segmented body parts. For this purpose we are using multivoxel pattern analysis to test for shared neural coding of the full-body illusion when it is driven by congruent visuo-tactile stimulation of the hand, the trunk or the leg respectively. Preliminary results indicate that of the three regions mentioned above, only the left PMv seems to contain voxels that show nearly identical BOLD activity patterns for the three body parts. In addition to these 'whole body' multisensory voxels however, we also found voxels that seem to show somatotopic patterns of activity, i.e. that differentiate between the conditions in which the full-body illusion is driven by stimulation of different body parts. We found these voxels to be located in the anterior IPS and the putamen, and their multivoxel patterns of BOLD activity suggest that they code for the multisensory integration related to different body parts exclusively in a somatotopic way. These results confirm and build on the results of the third fMRI experiment of Study III. Further data analyses employing psychophysiological interactions (PPI) or dynamic causal modeling (DCM) will be invaluable to further unveil the complex nature of the interplay between different brain areas that underlies the experience of a corporeal self.

Future lines of research

Electrophysiological studies in humans employing electroencephalography (EEG) or magnetoencephalography (MEG) would represent an important tool for addressing the binding problem mentioned in the discussion, and could possibly reveal the temporal relationship and connectivity pathways between the different brain areas involved in body ownership.

Electrophysiological studies in monkeys would also be invaluable for shedding further light on the neural interactions at play in the generation of body ownership, especially since they would allow simultaneous single cell recordings from multiple brain areas, measurement of local field potentials as well as multi unit recordings. An obvious challenge for such studies would be the adaptation of the full-body ownership illusion set-up for non-human primates, and in particular the reliable assessment of the potential illusory experience in monkeys. However, the successful development of such a set-up would represent a unique opportunity to study the causal relationships within the neural network underlying body ownership, as it would enable the selective deactivation of specific nodes of the network through precise brain lesions or optogenetics.

Lastly, pharmacological studies involving the rubber hand or full-body illusions could potentially elucidate the role played by individual neurotransmitter systems in the process of self-attribution of a body.

Body swapping in clinic and industry

The perceptual full-body ownership illusion provides a novel tool for a broad spectrum of clinical, scientific, and industrial applications. For example, the set-up developed in the course of this PhD research has been used to investigate the nature of telescoping of phantom limbs and associated phantom pain in amputees (Schmalzl and Ehrsson 2011; Schmalzl et al 2011). Currently in preparation is a series of research projects that will use this set-up for possible therapeutic applications in patients with eating disorders. In addition, the full-body ownership illusion has been replicated in virtual reality settings, showing that healthy participants can be induced to experience even the body of a computer generated avatar as their own (Slater et al 2009; Slater et al 2010). Further potential scientific, clinical and industrial applications range from social psychology (e.g. prejudice research) to clinical psychology (e.g. body dysmorphic disorder, gender identity disorder etc.), psychiatry (e.g. schizophrenia), neurology (e.g. neuropathic pain, somathoparaphrenia etc.), robotics, telepresence, virtual reality, and possibly even more. Exploring the full potential of the full-body ownership illusion and the full range of its applications as an experimental tool represents a possibly fruitful endeavor for a wealth of future studies to come.

7 NEW HYPOTHESIS OF BODILY 'MINENESS'

7.1 THE 'HARD PROBLEM' OF BODILY 'MINENESS'

'Why does the feeling which accompanies awareness of sensory information exist at all?' and 'Is consciousness reducible to its neural correlate?' are two essential questions that comprise the 'hard problem' in the study of consciousness (Chalmers 1995, 1996). Several theoretical and experimental approaches have attempted to provide answers to these questions and pinpoint the neural correlates of consciousness.

A common proposal of most theories of consciousness is that it relies on distributed representations in widespread fronto-parietal brain networks (Baars 1988; Baars 2002; Baars et al 2003; Dehaene et al 2006; Dehaene et al 1998; Dehaene and Naccache 2001; Dehaene et al 2003; Gaillard et al 2009; Rees 2007). In addition, a subset of theories specifically focuses on the binding of information within these brain networks through oscillatory neural activity (Crick and Koch 1990; Engel and Singer 2001; Singer 2001). One other theoretical framework equates consciousness with integrated information, which is defined as the amount of information generated by a complex of elements that goes beyond the information generated by its parts (Tononi and Edelman 1998a; Tononi and Edelman 1998b; Tononi and Laureys 2005). Another recent theoretical account further extended this notion, by postulating that consciousness is the result of self-directed social perception (Graziano and Kastner 2011).

Can any of these theoretical models be applied to specifically address the qualia of the bodily 'mineness'? As discussed above, the sensation of body ownership seems to arise from activity in a widespread cortical and subcortical network, with multisensory integration in fronto-parietal-subcortical regions playing a central role. This widespread cortical representation of the phenomenology of the corporeal self fits well with most of the theoretical models of consciousness, which in fact envision consciousness to also be the 'product' of wide spread information processing.

The fact that the body is always there, however, makes the qualia of bodily 'mineness' per se rather *tonic* than *phasic* in nature. Hence, it can be hypothesized that the conscious perception of the corporeal self is phenomenologically 'weak', i.e. not salient. At any given time, depending on specific contexts, we can become aware of distinct aspects of this experience, for example sensory sensations, motor output, proprio- or interoception, particular spatial, visual or cognitive information. Extensive further experimental research will be needed to reveal whether this process of bringing selective aspects of the bodily self into awareness is related to specific synchronized oscillatory activity in different sub-sets of the general widespread network, or whether it is more specifically linked to the mechanisms giving rise to social perception and cognition. Interestingly, one recent study involving electro encephalography reported that the experience of the rubber hand illusion is associated with inter-electrode synchrony in gamma band activity across the entire brain (Kanayama et al 2009). However, to date no other studies have confirmed these results in relation to body ownership.

Investigating the mechanisms underlying the qualia of the bodily 'mineness' is intrinsically difficult, and it is nearly impossible to envisage an experimental condition in which the experience of qualia as such could be ‘masked’ so it would not reach a level of conscious awareness. One such experimental condition would be the time window preceding the perceived onset of a body (part) ownership illusion. However, even this condition would have a serious limitation. Namely, even prior to experiencing the full-body or rubber hand illusions, participants have an implicit sense of ‘mineness’ of their actual body, which can’t be experimentally removed, and which can be assumed to be ‘transferred’ onto the new body. Nevertheless, the monitoring of the onset-time of illusory ownership of an artificial body or body part, and its relation to the subjective experience of qualia of bodily ‘mineness’, represents at least for now the most promising candidate for addressing this fundamental question.

7.2 SELF VS OTHER IN THE BRAIN

One remarkable property of the brain is its ability to code the motor behavior and intentions of other people. In a seminal study, (Di Pellegrino et al 1992) discovered the existence of so-called mirror neurons in the monkey brain, which fire both when a monkey executes a movement, and when it observes another monkey or a human being performing the same movement. Numerous fMRI studies conducted since then have suggested the existence of such mechanism also in the human brain, and demonstrated similar mirroring properties in broad spectrum of cognitive and sensory modalities (Blakemore et al 2005; Buccino et al 2001; Carr et al 2003; Gazzola et al 2006; Gazzola and Keysers 2009; Grafton et al 1996; Iacoboni et al 1999; Keysers et al 2004; Rizzolatti and Fabbri-Destro 2010; Singer et al 2004; Wicker et al 2003). Most of the early studies mainly focused on action recognition, motor learning and imitation (Gallese et al 1996; Rizzolatti et al 1996). Subsequently, the focus was also extended to the investigation of how the brain distinguishes mirrored from self-initiated actions (Agnew and Wise 2008; Avikainen et al 2002; Iacoboni et al 1999; Ishida et al 2010; Yoshida et al 2011). A proposed neural correlate of this differentiation is a modulation of the somatosensory cortices. For instance, Saxe et al (2006), found suppression of the BOLD signal in the primary somatosensory system, and concomitant enhanced activity in the right EBA, when participants observed body parts from a third person perspective. The authors suggested that the integration of such visual and somatosensory activity is informative for the discrimination between the self and the other. Contrary, another study found that hand actions and their observations were associated with enhanced activity in contralateral SI and a bilateral suppression of activity in SII, and concluded that a modulation of activity in these areas is likely to play role for self-other differentiation(Avikainen et al 2002). Furthermore, differential activity in the medial and lateral parietal operculum (SII) has been observed depending on whether the action was self generated or observed, suggesting that this area plays an important role in distinguishing executed from observed events (Agnew and Wise 2008). However, contralateral somatotopically organized activity in primary and secondary somatosensory cortices, as well as activity in the premotor and parietal cortices and the superior temporal sulcus have been found when healthy participants observed videotaped touched delivered to the face and neck of another person(Blakemore et al 2005). While further research is needed to clarify the reason for the contrasting patterns of SI and SII activation found in these different studies, their findings converge in underlining the importance of the somatosensory system when it comes to agent vs. observer discrimination.

Further insights into the intricate mechanism of self-other discrimination come from electrophysiological studies in non-human primates. For example, a study revealed the existence of bimodal neurons in the ventral intraparietal area as well as the area 7b of the monkey brain, whose receptive fields are anchored on the monkey's body but that also discharge in response to visual stimuli approaching corresponding parts of the experimenter's body (Ishida et al 2010). Importantly, the visual receptive fields of these neurons covered an area of approximately 30 cm from the experimenter's body surface, which corresponds to the spatial dimensions of peripersonal space (Graziano and Gross 1994; Rizzolatti et al 1981). The authors suggested that these neurons might play an important role for the spatial matching between one's own and someone else's body, for action recognition and for imitation.

Another interesting recent study found that a set of mirror neurons in the monkey's ventral premotor cortex preferentially responded to observed action performed within the peripersonal space of the monkey, whereas another set of mirror neurons in the same area preferentially responded to observed actions performed in the monkey's extrapersonal space (Caggiano et al 2009). In addition, while some of these spatially selective mirror neurons encoded space according to a metric representation, others seemed to encode it in operational terms, i.e. they modulated their firing rate depending on the monkey's actual possibility to interact with the object. None of these neurons had somatic receptive fields, i.e. they were not multisensory in nature.

One other recent elegant study has found the neural mechanisms of self-other differentiation to encompass areas in the medial frontal cortex as well (Yoshida et al 2011). The results of this study provide compelling evidence for the existence of a large population of neurons in the dorsomedial convexity region (i.e. pre-supplementary motor area), which selectively respond to actions performed by a partner monkey, while being silent throughout the execution of identical self-generated actions. Moreover, about one third of these 'partner-type' neurons were selective for the position of the action target, whereas only a small percentage responded to visual features of this target (i.e. the color). Within the same area however, the authors also found self-type neurons which seem to selectively code self generated actions, as well as and non-differential neurons (i.e. mirror neurons) which respond to both performed and observed actions. These intriguing findings suggest that the medial frontal cortex plays an important role in coding higher order agent-related information.

7.3 A NOVEL HYPOTHESIS OF 'MINENESS TAGGING' MECHANISM

Given the variety of neurons in the ventral premotor, intraparietal and medial frontal cortices, as well as their differential multisensory, mirror and agent related properties, an interesting question arises: Could it be that instead of belonging to different neuronal systems, all these neurons are part of the same frontoparietal network which jointly codes the agent (self vs. other), the space of action (near vs. far), the behavioral relevance of the object location (reachable vs. non-reachable) and the type of behavior (executed vs. observed)? In other words, in theory it is possible to hypothesize that based on the pattern of activity of subsets of these populations of neurons, the brain is able to extract the complex information necessary to code the self and other in a shared sensorimotor environment. For example, the sensation of ‘self-agent’ would be elicited through synchronized firing of populations of multisensory neurons in key multisensory areas with visual receptive fields restricted to the own body, and concomitant coupled firing of: a) canonical neurons in motor and premotor areas which code self-generated actions, b) sub-populations of mirror neurons which code for nearpersonal space and object reachability, and c) neurons in the medial frontal cortex which selectively code the self-agent of motor behavior). In addition, synchronized input from somatosensory, insular, and higher order visual (i.e. EBA) cortices, as well as activity within the memory and attention systems could further contribute to the self-attribution of the action. Conversely, the sensing and understanding of ‘other-agent’ would be elicited through synchronized firing of sub-populations of multisensory neurons with visual receptive fields covering the corresponding parts of the other individual’s body, and concomitant coupled firing of: a) mirror neurons which selectively code the distance between the self and the other, and b) populations of ‘partner-type’ neurons in the medial prefrontal cortex. And again, a potential modulation in somatosensory, insular, and higher order visual cortices could further strengthen the neural representation which specifically codes that the agent of the behavior is somebody else.

In sum, differential activity of this widespread self-other discrimination system can be hypothesized to represent a sort of neural ‘tagging’ mechanism, responsible for classifying sensory-motor experiences as either related to the self (by labeling the qualia of it as ‘mineness’) or the other (by labeling the qualia of it as ‘otherness’). Specifically, what could be the case is that coupled activity (possibly in the gamma band) in neuronal populations across this shared self-other network selectively signals the self vs. the other with respect to ownership of bodily perceptions and actions.

In addition however, it also can be hypothesized that a concomitant modulation of the neural activity within the TPJ, specifically the superior temporal sulcus, may play an additional important role within this ‘tagging’ system. In fact, lesions within the TPJ have been found to be associated with erroneous inference of other’s beliefs (Samson et al 2004), erroneous perception of self localization (Blanke et al 2004; Blanke et al 2002), and failures in spatial attention (Friedrich et al 1998; Ptak and Schnider 2010). Moreover, functional imaging studies in humans have found TPJ activation to be associated with experimental paradigms involving perception of gaze direction and biological movement (Grossman et al 2000; Pelphrey et al 2005; Puce et al 1998), perception of others’ movement intentions (Blakemore et al 2003; Pelphrey et al 2004; Vander Wyk et al 2009), multisensory shifts in attention (Macaluso and Driver 2001; Macaluso and Frith 2002) as well as transition detection and sensory saliency (Downar et al 2000, 2002). Importantly, one recent study suggests that at least in the right TPJ there are distinct sub-regions involved in attention orientation tasks and Theory of mind tasks (Scholz et al 2009). Hence, it can be speculated that differential activity within the TPJ, or selective damage to specific sub-regions of it, can affect the correct labeling of beliefs, intentions or sensory-motor experiences with respect to their owner or agent.

7.4 HOW CAN THIS 'TAGGING' HYPOTHESIS BE TESTED?

Ideally, testing of this novel hypothesis proposed above would involve an experimental setup that enables the selective impairment of the activity patterns across this global network, and the consequent monitoring of the resulting behavior and conscious experience. That is, according to this hypothesis lesions or abnormal activity in the patterns of activity that selectively code for the self (agent, perceiver) should lead to impaired sensations of agency, erroneous attribution of sensory-motor information to others (i.e. erroneous qualia of 'otherness'), or a more general failure to experience body ownership and process higher order cognitive self-related information. Conversely, lesions or abnormal activity patterns affecting the neural representation of the other (agent, perceiver) could lead to erroneous self-attribution of others' sensations or actions, or more general failures to process others' actions, beliefs or intentions.

In this respect, it is of particular importance to consider cases of neurological patients with specific disturbances of the 'mineness' vs. 'otherness' qualia. For example, Blakemore et al (2005) reported a case of a woman who, when observing another person being touched, experienced tactile stimulation on the equivalent parts of her own body. Importantly, the patient did not have any other neurological disturbances, nor did this 'mirror-touch' synesthesia occur when the patient observed objects being touched. Compared to healthy controls, her brain activation associated with the observation of videotaped tactile stimulation of another person's face and neck, was characterized by a significant increase in activation in primary and secondary somatosensory cortices and the left ventral premotor cortex, as well as an additional activation in the anterior insula. In the context of the speculations outlined above, it can thus be hypothesized that abnormal patterns (i.e. increased levels) of neural activity in some of the key areas of the distributed self-vs.-other brain network (in particular the ventral premotor and somatosensory cortices as well as the interoceptive system), can lead to the erroneous 'mineness' experience of others' tactile sensations. It would be of particular interest to perform whole brain multi-voxel pattern analysis to characterize the neural activity underlying mirror-touch synesthesia, with respect to that underlying the observation of tactile stimulation applied to external objects or one's own body.

Examples of erroneous 'otherness' labeling in clinical populations include cases of somatoparaphrenia and schizophrenia. As discussed above, the clinical picture of somatoparaphrenia is complex and variable, sometimes also involving white matter lesions. However, the disorder has most commonly been found to be associated with damage to cortical and subcortical regions including fronto-parietal areas, the insula, the basal ganglia, as well as fiber tracts to and from the ventral premotor cortex. Hence, it can be argued that even selective damage to parts of the widespread self-vs.-other brain network and the resulting disturbance in the global information processing and patterns of activity can lead to erroneous misattribution of own body parts to another individual, and to the consequent erroneous experience of 'otherness'. In terms of patients with schizophrenia, it would be of particular interest to compare the neural activity associated with delusions of influence (i.e. movements of the own hand that are attributed to other agents), to that of other auditory or verbal hallucinations. A number of studies have already proposed a link between schizophrenia and disturbed functionality in the mirror neuron system (Arbib and Mundhenk 2005; Enticott et al 2008; Iacoboni and Dapretto 2006). However, further research would be needed to determine whether delusions pertaining to the ‘domain’ of body ownership and agency attributions in particular, might be caused by specific malfunctions of the more general self-vs.-other ‘tagging’ network in the brain.

7.5 CONCLUSION

In sum, as suggested by the empirical data presented in this thesis, the sensation of owning a body seems to be coded by multisensory neurons in the ventral premotor cortex, the intraparietal area and the putamen. On the basis of our data as well as other relevant literature discussed above, I speculate that the conscious qualia of body ‘mineness’ further relies on the activity of an extended brain network that supports self consciousness. In addition to the multisensory visuo-somatic areas, this network would also include the mirror neuron system, the EBA, the sensory-motor system, the insular cortex, the limbic system, as well as areas related to memory and attention in the medial frontal and parietal lobes. I further speculate that synchronized firing (possibly in the gamma band) of specific subpopulations of neurons belonging to this larger brain network could be a driving mechanism for the subjective qualia of ‘mineness’. In other words, according to this hypothesis bodily ‘mineness’ would arise when multisensory integration giving rise to the sensation of body ownership is accompanied by information processing in the extended brain network that supports self-agent perception and self-consciousness. Finally, I put forward the novel hypothesis of a self-vs.-other ‘tagging’ brain mechanism, which relies on the activity of multisensory and mirroring systems, and which is responsible for self-other distinction and agency attribution.

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